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Potential Effects of Climate Change on the Distribution and Migration of European Breeding Migratory Birds

by

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2009

Submitted in partial fulfilment of the requirements

for the degree of Doctor of Philosophy

Abstract

Aim: This thesis aims to investigate the potential impacts of climatic change on Afro-Palaearctic migratory birds by investigating simulated changes in breeding and non-breeding distribution.

Methods: Generalised Additive Models were used to determine those climatic variables that produced the most robust species distribution models. Tests on the performance of three regression-based techniques were undertaken and consensus modelling framework was subsequently chosen. This framework was used in conjunction with three general circulation models and two emission scenarios to model the future distributions of Afro-Palaearctic migratory birds. Changes in both breeding and non-breeding range and migratory distance were examined for groups of species. A vulnerability index was created to indicate those species that were most vulnerable to climate change. Finally, changes in recent population trends observed on the European breeding grounds were related to simulated climatic suitability to investigate the role of climate in recent population changes and determine the vulnerability of populations to climate change. This analysis also enabled a partial validation of species distribution models.

Results: The results indicate differential change on the breeding and non-breeding grounds for many species. For many migratory birds a progressive separation of the two ranges is projected, potentially increasing migratory distances in future. However, for some species newly suitable climatic areas may provide non-breeding areas closer to the breeding range, enabling species to adapt to climatic change. Trans-Saharan migrants, species residing in dry environments as well as montane and coastal species are projected to be most vulnerable to climatic change. Although a link between population trends and climatic suitability could be found, the results indicated, as might be expected, that climate is only one of a number of factors potentially contributing to population changes

Conclusion: This thesis gives the first broad analysis of the likely direction and magnitude of change of the distribution of migratory birds to climate change, when only climate is considered. The challenge ahead is to refine these coarse scale models to include habitat and demographic data so as to provide more realistic estimates of change and improve conservation strategies that aim to support species under climate change.

Declaration

The material contained within this thesis has not been submitted for a degree at the University of Durham or at any other university. The research reported in this thesis is the work of the author unless indicated otherwise.

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Table 1: List of species named in the text (alphabetical order)

Species	Common name
Accipiter nisus	Sparrowhawk
Acrocephalus arundinaceus	Great reed warbler
Acrocephalus griseldis	Basra reed warbler
Acrocephalus paludicola	Aquatic warbler
Acrocephalus schoenobaenus	Sedge warbler
Acrocephalus scirpaceus	Reed warbler
Anthropoides virgo	Demoiselle crane
Aptenodytes forsteri	Emperor penguin
Anas platyrhynchos	Mallard
Apus Apus	Common swift
Ardea cinerea	Grey heron
Ardeola ralloides	Squacco heron
Bubulcus ibis	Cattle egret
Bufo marinus	Cane toad
Burhinus oedicnemus	Stone curlew
Buteo buteo	Common buzzard
Carpodacus purpureus	Purple finch
Carpospiza brachydactyla	Pale rockfinch
Cercotrichas galactotes	Rufus bush robin
Chlidonias hybridus	Whiskered tern
Cicona cicona	White stork
Cicona nigra	Black stork
Cinclus cinclus	White-throated dipper
Circus aeruginosus	Marsh harrier
Circus macrourus	Pallid harrier
Circus pygargus	Montagu's harrier
Coccyzus americanus	Yellow-billed Cuckoo
Delichon ubrica	House martin
Dendroica caerulescens	Black-throated blue warbler
Egretta alba	Great egret
Egretta garzetta	Little egret
Emberiza cineracea	Cinereous bunting
Erithacus rubecula	Red robin
Fagus crenata	Japanese beech
Falco cherrug	Saker falcon
Falco eleonorae	Eleonora's flacon
Falco naumanni	Lesser kestrel
Falco peregrinus	Peregrine falcon
Falco subbuteo	Hobby
Falco tinnunculus	Kestrel
Falco vespertinus	Red-footed falcon
Ficedula hypoleuca	Pied flycatcher
Ficedula semitorquata	Semi-collared flycatcher
Fulmarus glacialis	Northern fulmar
Gallinula chloropus	Moorhen
Geronticus eremita	Bald ibis
Grus grus	Common crane
Gyps fulvus	Griffon vulture
Hieraaetus pennatus	Booted eagle
Hippolais languida	Upcher's warbler

Table 1 continued

Species	Common name
Hippolais pallid	Olivaceous warbler
Hirundo atrocaerulea	Blue swallow
Hirundo rustica	Swallow
Hyla arborea	Tree frog
Larus fuscus	Lesser black-backed gull
Larus genei	Slender-billed gull
Limicola falcinellus	Broad-billed sandpiper
Locustella naevia	Grasshopper warbler
Luscinia svecica	Bluethroat
Marmaronetta angustirostris	Marbled duck
Melospiza melodia	Song sparrow
Megrus serrator	Red-breasted merganser
Merops apiaster	Bee-eater
Monticola solitarus	Blue rock thrush
Motacilla flava	Yellow wagtail
Muscicapa striata	Spotted flycatcher
Neophron percnopterus	Egyptian vulture
Netta rufina	Red-crested pochard
Nycticorax nycticorax	Black-crowned night heron
Pandion haliaetus	Osprey
Parus major	Great tit
Phoenicurus ochruros	Black redstart
Phoenicurus phoenicurus	Redstart
Phylloscopus collybita	Chiffchaff
Oenanthe oenanthe	Northern wheatear
Oenanthe xanthoprymna	Red-tailed wheatear
Rallus aquaticus	Water rail
Riparia riparia	Sand martin
Saxicola torquatus	Common stonechat
Scolopax rusticola	Woodcock
Spizella pusilla	Field sparrow
Sterna caspia	Caspian tern
Sterna sandvicensis	Sandwich tern
Sylvia atricapilla	Blackcap
Sylvia communis	Whitethroat
Sylvia hortensis	Orphean warbler
Sylvia melanothorax	Cyprus warbler
Sylvia sarda	Mamora's warbler
Sylvia undata	Dartford warbler
Tachybaptus ruficollis	Little Grebe
Tachymarptis melba	Alpine swift
Tringa totanus	Redshank
Troglodytes troglodytes	Wren
Turdus merula	Blackbird
Turdus torquatus	Ring ouzel
Vanellus vanellus	Lapwing

1. Introduction

Climate change and its effects on biodiversity are of great current concern. Many studies have already documented and demonstrated changes in climate and the effects of these changes on species (King, 2005; McCarty, 2001; Parmesan and Yohe, 2003; Root *et al.,* 2005; Walther, Berger and Sykes, 2005; Walther *et al.,* 2002). The high likelihood that this global climate change is set to continue (IPCC 2001) has led to the development of climate impact studies, which simulate future climatic scenarios based on what is known of climate dynamics and economic and political scenarios (IPCC, 2001; Nakicenovic, *et al.* 2000) and then, in some cases, predict the consequences for species.

Birds have been considered as indicators of ecosystem health (Gregory *et al.,* 2005) and as such have been used as indicators of change (Eaton *et al.,* 2005; Gregory *et al.,* 2009). It is, therefore, appropriate to examine the effects of climate change on this taxon. Many studies have already been conducted on this subject, though few have specifically looked at the consequences of global climate change on the distribution and migration of migratory birds. Migration is a common strategy among birds, particularly for species in temperate regions, to cope with seasonal variability in food supplies. Around 70% of the breeding bird species of the Western Palaearctic are migratory, 30% undertaking long-distance migrations to sub-Saharan Africa (Snow and Perrins, 1998; Moreau 1972). Migration is a complex process driven by ecological, physiological and biogeographic factors (Alerstam *et al.,* 2003; Berthold, 2001; Berthold and Helbig, 1992; Newton, 2008). It is often strongly linked with changes in temperature and prey availability (Berthold, 2001; Moreau 1972; Robinson, *et al.* 2005). Therefore, the current and predicted future changes in climate (Barker *et al.*, 2007) have the potential to affect substantially migratory bird species, especially long-distance migrants.

The convention on the Conservation of Migratory Species (CMS) recognises that signatory states have a duty to protect migratory species that live within, or pass through their jurisdictional boundaries. Moreover, it states that effective population management requires concerted action from all states in which a species spends any part of its life-cycle (CMS, 2006). For effective management, states would need to know how climatic change is to affect migratory species.

This thesis aims to give some insight into how climate change may affect migratory birds in terms of their distribution on both the breeding and the non-breeding grounds,

migratory distance, changes in species richness and migratory strategy. It also aims to answer whether projected climate change will affect species with differing migratory strategies differently, and which species are most likely to suffer under the projected climatic change. These questions are addressed using species distribution models and concentrate on Afro-Palaearctic migratory birds; those birds with breeding distributions within Europe and with non-breeding ranges within the Western-Palaearctic and Africa.

In the first part of this thesis (Chapter 2), a review of the relevant literature on migratory birds, climate change and species distribution models, is presented. This lays the foundation for a number of research aims and questions that are to be answered in the following chapters.

In a preliminary study, Doswald *et al.* (2009) modelled the breeding and non-breeding ranges of 17 *Sylvia* Warblers. This group of species was chosen because they have a diversity of migration patterns and have a diversity of range extents, many of which are wholly within the Western Palaearctic. In this preliminary study, two modelling methods and four bioclimatic[1] variables were tested (see Appendix I; Doswald *et al.* 2009). This ground work highlighted the necessity of exploring model selection and robustness, and of comparing different methodologies for modelling species' distributions. Chapter 3 explores which bioclimatic variables best describe the migratory species' breeding and non-breeding distributions and the importance of model robustness in the prediction of species' distributions. Chapter 3 also compares three widely used modelling methods for building species distribution models. Finally, it presents the models for the migratory birds presented in this study and asks whether species' ecological characteristics determine how well their ranges can be modelled.

In Chapter 4, species' ranges are projected onto future climate scenarios. The first part of this chapter examines the differences in projected range change among modelling methods and discusses ensemble forecasts. In the second part of Chapter 4, the preliminary study of Doswald *et al.* (2009) is extended to all Afro-Palaearctic migrants (see Appendix I). Section 4.2 presents summary statistics on relative range changes, changes in migratory species richness and changes in migratory distance for migratory species as a group.

Doswald *et al.* (2009) postulated that climate change would affect species of differing migratory strategies differently: specifically 1) there might be differences in response to climate change among long-distance or short-distance migrants; 2) that trans-Saharan migrants would face increased migration distance between the breeding and the non-breeding

[1] The variables are bioclimatic variables rather than purely climatic because they include a measure of soil water availability.

compared to resident/short distance; and 3) species with small geographical ranges on either the breeding or non-breeding grounds would suffer more from the effects of climate change due to less range overlap with regions of suitable future climate. We found no consistent difference in mean future range extents or overlaps between trans-Saharan migrants and residents/local migrants. Moreover, we found that changes in migration distance between current and future simulations were not significantly different between long-distance migrants and short-distance migrants/residents; but there were differences between wide-spread and range restricted species. However, the number of species used in the study (17) was too limited to produce general conclusions about long-distance versus short-distance migrants. The question of whether there are differences between migratory groups is addressed in the final section of Chapter 4 and applied to all European breeding migratory birds. Potential changes in migratory strategy and residency are also explored using simulated changes in species' distributions.

Chapter 5 focuses on species' and populations' vulnerability to climate change. In the first part of Chapter 5, an index of impact of climate change is created, based on changes in range and migratory distance. This categorises those species that are the most vulnerable to future climate change. The chapter also discusses how much can be inferred from species distribution models with regards to extinction risk. The questions arising from this section are explored in the second section of Chapter 5, which asks specifically whether inferences about species' abundances can be made using species distribution models. Although changes in species' distribution in response to climatic change have been observed (see Chapter 2), changes in population numbers are more difficult to attribute to climate change. In this section, recent population changes are related to changes in climatic suitability as modelled by the methods detailed in Chapter 3. This provides a partial validation of the species distribution models and discusses other factors involved in population change. The final part of this chapter relates recent population change to future vulnerability from climatic change, as typified in the index. This section also discusses how much inference can be made regarding population change.

Finally, Chapter 6 sets the results of this study in the wider context. First, the findings of this thesis are synthesised and the results are discussed in terms of other studies. Second, the uncertainty and limitations are outlined and the likelihood of changes happening as projected is discussed in an evolutionary context. Finally, future research avenues and challenges are outlined.

2. Background and Aims

The relationship between climate and birds' geographical distributions, as well as with their migration (Moreau 1972; Root 1988a; Root 1988b), has lead researchers to question how current and future climate change may influence species' range boundaries (Root & Schneider 1993). Moreover, how climate change may influence migratory species has been of concern. Indeed, Berthold (2001) postulated that long-distance migrants may be particularly affected by climate change as migrants rely on spatially separated areas that are often bio-climatically different (e.g. Eurasia and Africa) and that are affected by different processes and drivers of change such as agricultural intensification in Europe and desertification in Africa. Long-distance migrants are often also dependent on stopover sites during migration. The effects of climate change on all these critical areas are unlikely to be uniform and will be exacerbated by other drivers such as habitat loss. Indeed, the world's landscape has already been altered through anthropogenic intervention and is likely to continue to change with human population growth and human reaction to the effects of global warming. The anthropogenic landscape is likely to interact with climate change in a yet unknown way and impact on species. This present study examines the current knowledge surrounding climate change and migratory birds and the models used to study the impact of climate change on species.

Initially, I will give some background to Afro-Palaearctic migrant birds including how climate affects birds and recent trends in migrant populations. Following on from this, I will consider current climate change, specifically in Europe and Africa and the effects of such change on migrant birds. In a third section, I will give an overview of climate modelling and of the predicted future climates for Europe and Africa. Then the methods for predicting the effects of future climate change will be reviewed and the current predictions for birds and other species residing in Europe and Africa will be considered. This will lead to the formulation of aims and research questions to be dealt with in the subsequent chapters.

2.1 Climate Change and Migratory Birds

2.1.1 Afro-Palaearctic Migrants

Afro-Palaearctic migrant birds typically breed in Eurasia and winter in Africa (Moreau 1972). There are 215 such species, most of which migrate to sub-Saharan Africa (Moreau 1972; Fry, 1992; Salewski and Jones, 2006; Newton, 2008; Walther *et al.,* 2004). Migration is a response to seasonality, a to-and-fro movement following the environmental conditions and the resources needed by the birds to survive (Berthold, 2001). Indeed, the Palaearctic winters do not provide the resources (e.g. insects) that the birds need, so they head south at the end of the Palaearctic summer (Moreau 1972; Fry 1992). Sub-Saharan Africa offers a suitable climate, resources and less stresses than winter on the breeding grounds (Fry, 1992). Migration is a common phenomenon in birds as well as in other animal groups (Alerstam *et al*., 2003), with migrant bird species, including Afro-Palaearctic migrants, in nearly all orders. There have been many ecological reasons put forward as to why migration should be such a successful strategy, such as reduced competition and access to preferred food sources (Fry 1992), when spending so much energy and time on migration seems counter-intuitive (Alerstam *et al.,* 2003). Many migrant species are successful, especially those that are partial migrants such as *Sylvia atricapilla*[1], a species that has seen increases in population in recent decades (Birdlife International, 2004a).

Most migratory species show high site fidelity in their breeding and non-breeding quarters (also termed goal areas) and stopovers (Berthold, 2001; Fransson *et al*. 2005; Markovets and Yosef, 2005). In general, species winter in similar habitats to those they breed in (Moreau, 1972; Fry, 1992; Telleria and Perez-Tris, 2003). Markovets and Yosef (2005) examined the winter site fidelity of *Luscinia svecica* at Eilat, Israel, for six seasons. Over their study period they recaptured 37.1% of marked birds. This result indicates high site fidelity when the difficulty in trapping and re-trapping birds is accounted for. Similar results were found for *Ficedula hypoleuca* in West Africa (Salewski *et al.,* 2000). There is less evidence for site philopatry in stopovers, although some areas have been identified along migration routes as consistent staging areas (Nolet and Drent, 1998). A study by Fransson *et al.* (2005) examining the distribution of seven passerine species in the eastern Mediterranean region (a passing point for many Afro-

[1] All common names for each species cited in this thesis can be found pages xvi to xvii.

Palaearctic migrants) suggests, though does not prove, that faithfulness to stopover sites may be a common pattern. High site fidelity has important implications for the conservation of migrant birds as the elimination or alteration of these sites could have negative impacts on these species. Some populations within a species also show strong connectivity[2] between the breeding and non-breeding areas. Procházka *et al*. (2008) investigated migratory connectivity of *Acrocephalus scirpaceus* by analyzing sub-Saharan ringing recoveries and stable isotopes in feathers grown in Africa. They found a strong connectivity with two main clusters representing populations taking two main migratory routes and establishing distinct winter quarters: South-West and South-East. The East – West divide is a common phenomenon among migratory species and may help identify some species' non-breeding ranges.

Indeed, the breeding areas of most Palaearctic-African migrant birds are well known but their non-breeding quarters in Africa are not (Sanderson *et al.,* 2006; Walther *et al.,* 2004, Walther *et al.,* 2007). Information is sketchy and unevenly distributed among species. General information about the non-breeding habitat of some migrants exists (e.g. Jones *et al.,* 1996; Morel and Morel, 1992; Pearson and Lack, 1992) and recently the Zoological Museum, University of Copenhagen has collated all information on the distribution of Palaearctic-African migrant birds in Africa (Walther *et al.,* 2004) while BirdLife International has set up a bird database including species' distribution (BirdLife International World Bird Database). About a quarter of all European migrants winter in the Sahel, a region that is also an important staging area for many trans-Saharan migrants (Jones *et al.,* 1996). With a few exceptions, migrants do not winter in equatorial rain forest. Instead, they mainly utilise heterogeneous open habitat (Salewski and Jones, 2006) in savannah type regions (Leisler, 1992).

Outward migration usually occurs between July and November (Jenni and Kéry, 2003) and return migration from March to May (Ahola *et al.,* 2004; Sparks *et al.,* 2005). There is a semi-distinct divide between East and West African non-breeding quarters marked by the flyways used by migrants with, in general, western populations of birds migrating to West Africa and eastern populations migrating to East Africa (Erni *et al*., 2005). Movement between goal areas is accomplished using refined orientation mechanisms, an adapted physiology, endogenous programmes (see Berthold 2001; Berthold and Helbig, 1992; Berthold *et al.,* 1992; Piersma, 1998) and the right environmental conditions (wind, no adverse weather, migration routes and refuelling areas). Selective breeding experiments with *Sylvia atricapilla*, in which either

[2] Migratory connectivity is a term used to describe the relationship between migratory species and geographic regions at different points during the year (Webster *et al.* 2002)

completely sedentary or completely migratory populations were bred from partial migrant populations (Berthold and Helbig, 1992; Berthold *et al.,* 1992), have given evidence that, for some species, migration behaviour and direction (shown through orientation chamber experiments) is genetic. However, other studies have also shown that phenotypic plasticity allows flexibility in migration strategies (Crick, 2004; Sutherland, 1998; Vähätalo *et al.,* 2004).

Afro-Palaearctic migrants have to cross two major ecological barriers between their goal areas: the Sahara desert and the Mediterranean Sea. Only a few species have the capabilities to cross these on a non-stop flight (Biebach *et al.,* 2000). The majority of birds have intermittent migration between goal areas for resting, i.e. staging, or resting and refuelling, i.e. stopovers (Bairlein, 1992; Biebach *et al.,* 2000; Nolet and Drent, 1998). Stopovers are vital for migrant birds because their physiology, and environmental conditions constrain how much energy (stored mainly as fat) they can carry (Berthold, 2001; Newton, 2008).

Of major interest to ornithologists are the cues used by migrants for the onset of migratory behaviour. It is generally assumed from the study of captive birds that the onset of migratory activity is controlled by endogenous programmes (Berthold, 2001). The fact that the length of the breeding season does not change even when birds arrive earlier on the breeding grounds (Cotton, 2003; Jenni and Kéry, 2003) corroborates that there are endogenous controls to the onset of migration. However, the environment constantly interacts with and impacts on species and, as such, the circannual rhythm is also likely to be an important factor in the control of migration (Berthold, 2001). Indeed there is evidence that photoperiodic cues are important for the onset of migration (Coppack *et al.,* 2003; Gwinner, 1990; Kok *et al.,* 1991). In many species, climate is important in determining phenological events (McCarty, 2001) and there is mounting evidence that it plays a role in (migrant) bird biology and ecology (Ahola *et al.,* 2004; Cotton 2003; Crick, 2004; Devictor, *et al.* 2008; Gordo and Sanz, 2008; H-Acevedo and Currie, 2003; Marra *et al.,* 2005; Parmesan and Yohe, 2003; Robinson *et al.,* 2005a; Saino *et al.,* 2004a; Saino *et al.,* 2004b; Sanz, 2002; Vähätalo *et al.,* 2004; Walther *et al.,* 2002; Weatherhead, 2005; Winkler *et al*. 2002).

Climate and migrant birds

Climate and weather[3] are important to migrant birds for a number of reasons. First, at large geographical scales, climate shapes a species' distribution – a species' climate-space (Root, 1998a, 1998b; Costa *et al.,* 2008; H-Acevedo and Currie, 2003; Huntley *et al.,* 1995; Lemoine

[3] Weather is the short term and local climate variations. Climate is the broad average climatic conditions of an area.

and Böhning-Gaese, 2003). However, it must also be recognised that species' distributions are also limited by biotic factors, such as habitat, competition, persecution and predation. According to Root (1988b) these factors "fine-tune" species' biogeographical ranges at the continent scale. Climate affects species directly and indirectly. Species are physiologically constrained by certain climatic variables. Root (1988b) showed that many birds' winter ranges are constrained by temperature and are related to species' basal metabolic rate. Climate also influences the resources birds depend upon (Root 1998a). Second, local climate variations, i.e. weather, affects a bird's fitness and survival (Newton, 1998; Newton, 2007). Indeed, extreme weather events, such as drought (common in sub-Saharan Africa) or very cold spells, can severely reduce a population and have long lasting effects (Baillie and Peach, 1992; Peach *et al*., 1991; Saino *et al.,* 2004a; Watkinson *et al.,* 2004). Adverse weather conditions also delay migration departure and delay species *en route* through direct mechanisms, such as bad flying conditions, and indirect mechanisms, such as food availability (Alerstam, 2001; Berthold, 2001; Gordo and Sanz, 2008; Newton, 2007; Piersma and Lindström, 2004; Saino *et al.,* 2004b). Third, climate affects reproduction: warmer conditions induce earlier breeding and egg laying (Both and Visser, 2001; Robinson *et al.,* 2005; Weatherhead, 2005), increased egg and clutch size (Crick, 2004) as well as fledgling success (Crick, 2004; Sanz, 2002; Weatherhead, 2005). And fourth, there is evidence that climatic influences on bird phenology affects competition between species. Lemoine and Böhning-Gaese (2003) showed that there was a potential competitive relationship between resident and migrant birds in that climate during the winters influenced the relative numbers of resident and migrant birds. Intra-specific competition is also indirectly influenced by climate through the timing of arrival on the breeding grounds (Cotton, 2003; Sparks *et al.,* 2005; Vähätalo *et al.,* 2004). Arrival date can vary due to temperature cues on the non-breeding grounds (Cotton, 2003; van Noordwijk, 2003), climate *en route* (Ahola *et al.,* 2004; Hüppop and Hüppop, 2003; Rubolini *et al.,* 2005; van Noordwijk, 2003) or through large-scale climatic phenomena like the North Atlantic Oscillation (Hüppop and Hüppop, 2003; Stervander *et al.,* 2005; Vähätalo *et al.,* 2004).

The North Atlantic Oscillation (NAO) is a large-scale fluctuation in atmospheric pressure in the Atlantic Ocean that influences the climate and weather in parts of Europe, North America and Africa (Vähätalo *et al.,* 2004). The NAO index, the normalized pressure differences between the Azores and Iceland, describes meteorological conditions in winter and spring (Hüppop and Hüppop, 2003). Positive values are associated with warm moist winters, while negative values are correlated with cold dry winters in northern Europe (Hurrell, 1995). This index has been used

in a number of studies to explain the spring arrival in Europe of migrant birds (Ahola *et al.*, 2004; Anthes, 2004; Hubalek, 2004; Hüppop and Hüppop, 2003; Marra *et al.*, 2005; Sparks *et al.*, 2005; Stervander *et al.*, 2005; Vähätalo *et al.*, 2004) as well as laying date (Sanz, 2002; Weatherhead, 2005). Some studies have argued that the NAO affects the spring arrival of all migrant birds, including long-distance Afro-Palaearctic migrants, breeding in Europe (Forchhammer *et al.*, 2002; Hüppop and Hüppop, 2003; Stervander *et al.*, 2005), whilst others argue that the NAO only affects short- to medium-distance migrants (Both and Visser, 2001; Hubalek, 2004; Nott *et al.*, 2002; Tryjanowski *et al.* , 2002). It is interesting that those studies that found a correlation between the NAO and spring arrival for long-distance migrants were those with study sites in the far North of Europe. This suggests that arrival time for these species is affected by the climate in Europe once the species are already in Europe and at stopovers. Alternatively, arrival time is affected by climate on the non-breeding quarters. Indeed, Cotton (2003) found that winter temperature in Africa was not correlated with winter NAO index and that arrival dates on the breeding grounds were correlated with temperature in sub-Saharan Africa. Saino *et al.* (2004b) and Gordo *et al.* (2005) also showed that weather (in particular rainfall) on the non-breeding grounds affected the spring arrival of trans-Saharan migrants not the climate on the breeding grounds. Indeed it is thought that the inter-annual fluctuations of spring arrival may be influenced by plant productivity and hence insect abundance on the African non-breeding grounds (Gordo and Sanz, 2008).

Recent trends

In a recent review, Sanderson *et al.* (2006) found that long-distant migrant birds were declining. More specifically, they found that species wintering in dry open habitats in Africa declined more than other long-distance migrants. Julliard *et al.* (2003) found that many common bird populations were declining in France. More specifically, south-biased species were doing better than north-biased species. In central Europe, a study found that whilst non-passerine bird richness remained stable from 1980 to 1990 and even increased between 1990 and 2000, passerine bird richness declined in both periods (Bauer *et al*., 2008).

Factors driving these declines could come from a number of fronts (goal areas and stopovers) and may be interacting in some way. Climate has been shown to drive long-term species' declines in the past. A major drought in Sub-Saharan Africa between1960-90s caused some populations to decline substantially (Baillie and Peach, 1992; Gordo *et al.*, 2005; Jones *et*

al., 1996; Marchant, 1992; Peach *et al.,* 1991; Wood, 1992). Additional drivers of change known to impact on migrants are habitat loss or deterioration, as well as land-use change such as agricultural intensification and drainage, and hunting (Berthold, 2001; Grimmet, 1987; Julliard *et al*., 2004; Sanderson *et al.,* 2006). The relevant contribution of each of these drivers to the current population trends in long-distance migrant birds is currently unknown and there is some conflicting evidence. Indeed, whilst the current decline of *Turdus torquatus* in northern Britain was significantly correlated with changes in summer climate (Beale *et al.,* 2006), population trends of birds residing in Spain were related to their habitat preferences rather than climate (Seoane and Carrascal, 2008). These results suggest that investigating the impact of climate change and its potential contribution to population change is a priority.

2.1.2 Climate Change

There is strong evidence that the climate has changed in the last century. Temperatures have increased world wide by about 0.6°C, rainfall has increased in some regions and decreased in others and there has been an increase in extreme weather events (Dore, 2005; Easterling *et al*., 2000; IPCC, 2001). Although some of these changes are part of the natural variability of climate, there is undeniable evidence that some of the changes in climate are due to anthropogenic forcing by amongst other things the increased release of greenhouse gasses (IPCC, 2001). These changes in the global climate have had impacts at the regional level on physical and biological aspects of the environment. Glaciers have retreated and arctic sea-ice extent and thickness have decreased (Cook *et al.,* 2005). This, along with thermal expansion, has resulted in annual global mean sea level rises of 1-2mm during the last decade (IPCC, 2001).

In the majority of Europe temperatures have increased by about 0.8°C this century during two major warming phases: 1900-40 and 1970 onwards (IPCC, 2001). In northern Europe (north of the Alps) precipitation has increased by 10-50% mostly during the autumn-winter period and precipitation has decreased in south and central Europe (Dore, 2005). These changes are not homogenous (Ahola *et al.*, 2004). Indeed, topography and land cover are also important factors in determining climate through various land-atmosphere interactions (Lioubimtseva, 2004; Maynard and Royer, 2004). These interactions are thought to be very important in regulating climate in Africa because precipitation variability, especially in the Sahel region, is difficult to explain (Hulme *et al.*, 2001; Nicholson, 2001). The African climate has varied considerably in the last 20,000 years. Around 5000 BP the climate was much more humid and the extent of desert was

much smaller. It was only around 2000 BP that a similar climate to today was reached (Nicholson, 2001). During the last century, Africa as a whole has warmed by 0.5°C with larger warming in the summer and autumn seasons (Hulme *et al.*, 2001). Rainfall variability in Africa is large with inter-annual, inter-decadal and multi-decadal patterns in rainfall making general trends difficult to discern. However, during the 20th century a general decrease in annual rainfall was observed (Dore, 2005; Gordo *et al.*, 2005; Hulme *et al.*, 2001; Nicholson, 2001), and a drop in precipitation of about 20-40% in the Sahel region (Maranz, 2009), causing widespread concern about irreversible desertification after the severe droughts between the 1960s-1990s (Olsson *et al*., 2005). More recently, some observations point to a 'greening' of the Sahel. Indeed data have been collected through remote sensing studies that suggest increased vegetation in this region (Herrmann *et al.*, 2005; Olsson *et al.*, 2005). The causes of this greening are attributed to increased rainfall during the period 1982-2003 and possibly anthropogenic causes (Herrmann *et al.*, 2005), such as better land management or population retreat from rural to urban areas (Olsson *et al.*, 2005).

Ecological responses to climate change

Species' current distribution patterns are a result of both ecology and history (Crisci and Katinas, 2009). Evidence from the fossil record shows that some species have responded to past climate change through migration and changes in range (Botkin *et al*., 2007; Thuiller *et al*., 2008) before declining to extinction due to new inter-specific interactions (Liow and Senseth, 2007). It is thought this is because species move individualistically and not as a community (Shuttle, *et al*., 2007; Willis *et al*., 2007).

Observed changes in the ecology of species during the last century have been documented on different fronts: geographic range of species, phenology, community ecology, and population dynamics. These changes have been related to climate change in many studies. Some species have extended their range northwards and up to higher altitudes in apparent response to current warming (see McCarty, 2001; Parmesan and Yohe, 2003; Thomas and Lennon 1999; Walther *et al.* 2002). Many species are showing signs of earlier phenological events such as first leafing, the first appearance of insects, or bird breeding date (McCarty, 2001; Peñuelas *et al.*, 2002). This is of great concern to ecologists, because although many spring events occur with temperature change, other events occur with different cues such as photoperiod or endogenous programmes. This may lead to an asynchrony in species' interactions. Indeed, such a mismatch has been reported for a plant, insect and bird food web (Visser *et al.*, 2004; Visser and Holleman, 2001;

Visser *et al.,* 1998). Disruptions in marine ecosystems are also being observed (see Walther *et al.,* 2002) though it is difficult to determine with any certainty in the marine system whether climate is a direct or an indirect driver of change. The effects of global warming on population dynamics can be directly measured on ectotherms as their biology is often directly influenced by temperature. For example, the sex ratios of some species are being female-biased by warmer temperatures (Janzen, 1994; Weatherhead, 2005).

Events in the biosphere are the result of complex interactions between biotic and abiotic factors and attributing change in the biosphere to climate change and to human-induced climate change is difficult and, at best, correlative. However, when many separate studies show trends in the expected direction of change, correlative relationships have more credibility as causative relationships. Meta-analyses that include a wide variety of species and geographic locations are the best for establishing quasi-causal relationships from individual correlative studies. Parmesan and Yole (2003) argue that for a driver of change to be causal, changes should occur in the expected direction. Their meta-analysis shows that this is the case for 84% of species examined, providing evidence that climate change is a factor in the observed change occurring in the biosphere. Root *et al.* (2005) go a step further to provide evidence for a 'joint attribution'; they show that the changes seen are due not only to climate change but also to human-induced climate change.

Climate change and birds

There is gathering evidence that (migrant) birds have already started to respond to the warming that has been experienced over the past century. Although all the evidence is correlative and so does not necessarily indicate a causal relationship, the consistency of the evidence strongly points to climate change being at least in part implicated in the ecological change seen (McCarty, 2001). In the UK and North America, there is evidence that birds have extended their range northwards in response to global warming (Thomas and Lennon, 1999; Valiela and Bowen, 2003). This may have severe consequences for those species that are already at the northern limits of their range or for species experiencing an altitudinal shift (Robinson *et al.,* 2005). Contraction at the southern limits of species' ranges has not yet been witnessed although many species' populations are in decline in southern Europe (Birdlife International, 2004b). At the southern range boundary of a distribution, species may be limited by heat or water availability. Although temperatures have increased world wide, increases are more noticeable at the poles, and, in the developed world at

least, water is currently not lacking due to human intervention (e.g. irrigation). This may explain the current stability of the southern margin of species' distribution (Böhning-Gaese and Lemoine, 2004). There are very few studies investigating the processes occurring in the 'trailing-edge' of species' distributions (Thuiller *et al*., 2008) but there is some empirical evidence that climate change is driving extinction in some plant populations (Foden *et al*., 2007).

The projected sea level rise is likely to have drastic consequences for coastal birds' habitat due to coastal squeeze, though this is not currently a major problem (Piersma and Lindström, 2004; Robinson *et al.*, 2005).

Changes in breeding and migration phenology have been widely reported in recent decades. In most temperate regions there has been an earlier onset of breeding and egg laying across a wide range of bird species, migratory and resident, since the 1970s (Both and Visser, 2001; Crick *et al.,* 1997; Sanz, 2002). This is not a universal phenomenon with some bird species showing no change in response to global warming (Sanz, 2002). However, although the global climate has warmed by 0.6°C over the last century, climate and especially microclimate is not homogenous. Nonetheless these observed changes (or stability) in breeding phenology may lead to a mismatch between the timing of breeding and the timing of peak resource availability as Visser *et al.* (1998) and Peñuelas *et al.* (2002) have already demonstrated for some species. Recently, Both *et al.* (2006) have shown that the mismatches evidenced in Europe between caterpillar emergence and the timing of breeding of a long-distance migrant bird has led to population declines.

Numerous studies have reported that arrival on the breeding grounds has advanced in recent years (Hubalek, 2004; Hüppop and Hüppop, 2003; Sparks *et al.,* 2005; Stervander *et al.,* 2005; Tryjanowski *et al.,* 2002). Van Noordwiijk (2003) put forward three hypotheses for the earlier arrival of Palaearctic-African migrants on the breeding grounds: first, the departure date from Africa has not changed, but better conditions in Europe allow faster refuelling; second weather in Africa has also changed, which induces earlier departure; and third weather in Africa has not changed but micro-evolution has changed the cues used by birds in Africa. There exists evidence that could support every one of these hypotheses as outlined in the previous section. On the other hand, some studies report that long-distance migrants show no change in arrival date (Both and Visser, 2001; Jenkins and Watson, 2000) or even later arrival (Gordo *et al.,* 2005; Peñuelas *et al.,* 2002; Sanz, 2002). No change or later arrival to the breeding grounds could have serious consequences for the fitness of birds. Indeed, early arrival is beneficial for species (as long as weather conditions are favourable) because it may ensure less competition, access to

more resources and opportunity to lay more clutches (Drent *et al.*, 2003; Rubolini *et al.*, 2005). Moreover, later arrival could and has widened the phenological disjunction between a species and its food resources (Both *et al.*, 2006). Two hypotheses for these contradicting findings (earlier or later arrival) have been put forward by Gordo *et al.* (2005): first, the conditions in Africa drive departure time. Saino *et al.* (2004b) showed that conditions in Africa could delay a species' arrival in Europe. Second, arrival time could depend on conditions *en route* and availability of resources at stopovers. This second hypothesis is supported by two studies (Huin and Sparks, 2000; Tryjanowski *et al.*, 2002). However, it is likely that a combination of factors from both hypotheses lead to the different arrival times of the long-distance migrants. Miller-Rushing *et al.* (2008) suggest that reported changes in migration times may also be a methodological artifact. They found that changes in migration times depended on the unit measured as well as changes in cohort size. They also found links between migration times and climate for short distance and mid-distance migrants.

There are only a few studies that have looked at departure dates from the breeding grounds in relation to climate change. Cotton (2003) assumed that the departure date of migrants from the breeding grounds would be delayed. However, he found that the majority of species he looked at actually left earlier, so that there was no significant change in the time spent on the breeding grounds. Jenni and Kéry (2003) analysed the peak passage of 64 migratory birds in Switzerland between 1958 and 1999. They found that all long-distance migrants advanced their departure date from Europe, whereas many (though not all) short-distance migrants delayed their departure. This study inferred that these changes may benefit short-distance migrants but not long-distance migrants who may lose out from not having a prolonged breeding season. However, they also speculated that early departure from the breeding grounds may be due to a selection pressure to cross the Sahel early. Earlier departure could, therefore, be beneficial to long-distance migrants because conditions on the non-breeding grounds are good at the start of the non-breeding season but deteriorate later on (Fry, 1992; Salewski and Jones, 2006).

There has been much speculation about how climate-induced changes in habitat may affect staging, stopovers and fuelling in migratory birds (Bairlein and Hüppop, 2004; Robinson *et al.*, 2005). These aspects of migration are liable to be mainly affected by land-use change, habitat loss or deterioration in conjunction with climate change. Migrant birds may have to cope with reduced fuel or find other stopover sites. There is evidence that birds arriving at stopovers where food is depleted have had to do with reduced fuel or fly to other stopover sites (Nolet and Drent, 1998). Examining what this means for migrant birds is integral for future research.

Adaptation to climate change

In response to environmental change, species have to adapt, change their distribution or abundance, or go extinct. Berthold (2001) postulated that, under climate change, partially migratory species would become resident because warmer climates allow overwintering on the breeding grounds. Resident species would increase under global warming and long-distance migrants would decrease from a combination of competition, loss of habitat and phenological miscuing. The extent to which long-distance migrants could adapt, or microevolve, and change their current migratory behaviour is not known. Berthold *et al.* (1992) showed that microevolution could take place rapidly, though a strong selective pressure would be needed. However, the capacity to evolve may depend on the strength of a species' migratory connectivity, i.e. how strong the links are between goal areas, genetic variation (Webster *et al.*, 2002) and phenotypic plasticity. Vähätalo *et al.* (2004) suggested that the observed relationship between the NAO and arrival dates was an indication that birds respond to change through phenotypic plasticity. However, the relationship between NAO and arrival dates is correlative and the true mechanisms behind this relationship are not known.

De Mazancourt *et al.* (2008) studied the interaction of evolutionary and ecological dynamics in a changing environment using a modification of the Levene model, which combines population dynamics and evolutionary dynamics models. They modelled the effect of environmental heterogeneity on evolution in a one species and in a multi-species environment. They found that as the number of species increased in a system, the less phenotypic evolution occurred. This was because, when competitive interactions were taken into account, species migrated to areas matching their initial phenotype rather than adapting to change. Although this study was a simulation, there is evidence from paleoecological and current studies that migration or dispersal to new areas is the favoured response to environmental change.

The fossil record shows that geographic extents of species are not static over geological timescales (Liow and Stenseth, 2007) and that species move individualistically and not as a community (Willis *et al*., 2007). Under environmental change many species respond by shifting their ranges by dispersal. However, dispersal is influenced by habitat heterogeneity, population dynamics and biotic interactions (Best *et al.*, 2007; Massot *et al.*, 2008). Suttle *et al.* (2007) experimentally studied the effects of changes in water availability (matching future projections) on species on grassland plots. They found that, initially, species' diversity increased as conditions became more favorable but, as the novel conditions persisted, the effects of the altered

community-level dynamics overshadowed individualistic responses leading to a decline in species' diversity. Brooker *et al.* (2007) also found a complex response to climate change due to biotic interactions. They used a spatially explicit modelling approach to explore potential effects of dispersal ability and biotic interactions on species' range shifting ability. They found that biotic interactions and the level of long range dispersal determined species' responses and, that they interacted with the rate of climate change to produce non-linear responses. Massot *et al.* (2008) analysed plastic dispersal using an experimental manipulation of a lizard population and meta-population model. The experiment showed that juvenile dispersal declined with increasing temperature, which would increase extinction risk according to their model. However, other species have shown increased dispersal tendencies under climate change (Massot *et al*. 2008). These contrasting examples show that evidence is currently ambiguous.

Intra-specific competition may also affect species' ability to shift ranges under climatic change. Best *et al.* (2007) investigated this using a simulation model incorporating competition, density dependence, dispersal and transient dynamics of habitat patches. Their results show that the type of competition (scramble or contest), density dependence and patch growth rate were all important factors in species' ability to shift their ranges in response to climate change. All these studies show that the response to climate change is complex and difficult to predict for any given species.

Coppack *et al.* (2003) argued that species would have to shift their non-breeding quarters north and decrease their migration distance so that photoperiodic cues used by migrant birds could bring these species to the breeding grounds earlier in conjunction with other phenological events. There is evidence of many species having changed their migratory routes and goal areas in the past and present (Sutherland, 1998). *Sylvia atricapilla* populations breeding in southern Germany and Austria and that usually winter in the Mediterranean now have a population wintering in the UK (Berthold, 2001), reducing their migration distance. Moreover, due to a different photoperiod in the north, *Sylvia atricapilla* also migrate earlier to the breeding grounds with the consequence that assortative mating occurs (Bearhop *et al.*, 2005). Although this indication that species can evolve new migration routes, along with evidence showing that species can adapt to changes in climate, is encouraging in terms of projected survival of these species, it also indicates the importance of other cues such as photoperiod and puts in question whether all species will be able to keep up with the current changes. Moreover, even if species could all change their migration patterns and routes there still is the uncertainty of whether there will be enough suitable habitat for species to shift their range, or space for these species to

establish into (Brooker *et al.*, 2007). Indeed, Travis (2003) used a model of habitat loss coupled with climate change to show that species would be more affected by climate change in a fragmented landscape.

2.1.3 Future Climates

Climate is complex and is regulated by many factors; predicting how it might change in the future is impossible without the use of global climate models (GCM). Climate models consist of a "set of mathematical equations that are solved using a three dimensional grid over the globe" (IPCC, 2001, p.48). They are based on fundamental physical laws (Randall *et al.*, 2007). The most comprehensive climate models are Atmosphere-Ocean General Circulation Models (AOGCMs) in which atmosphere circulation and ocean circulation models are coupled so that the variability and physical processes of these systems can be studied. AOGCMs are used to predict future climates as well as the rate of change (IPCC, 2001). The models most often used by scientists in Europe are those developed by the Hadley Centre, in particular HadCM2 developed in 1994 and HadCM3 developed in 1998. A major problem of many AOGCMs is that they become unstable (called climate drift) when simulating current climates (Gordon *et al.*, 2000; IPCC 2001). This problem was side-stepped in the past by using flux adjustments, i.e. adjusting the heat and water flux terms (IPCC 2001). Although this fixes the problem it does not improve the models. HadCM3, however, was created to overcome this problem. This AOGCM produces stable climate models without flux adjustment (Gordon *et al.*, 2000) and also provides better simulations (i.e. produces similar patterns to those observed) than its predecessor HadCM2 (Collins and Cooper, 2001). Since the Third Assessment Report, most AOGCMs no longer use flux adjustments and, in the Fourth Assessment Report (AR4), have been much improved in terms of their dynamical cores, their resolution, the number of processes included in the models and their parameterisation of the physical processes (Randall *et al.*, 2007). All AGOCMs, created by scientists around the world, perform slightly differently so that the uncertainty in predictions is evident (IPCC, 2001). However, when taken in conjunction, the mean of all models show better agreement with observed large-scale phenomena than single models because individual model biases tend to cancel each other out (Meehl *et al.*, 2007). The reliability of these models is considered high because 1) they are based on established physical laws, 2) they simulate important aspects of the current climate and 3) they can reproduce features of past climates (Randall *et al.*, 2007; Hegerl *et al.*, 2007). However, there are still significant features of the

climate that these new models cannot accurately reproduce, such as tropical precipitation, El Niño, the Southern Oscillation and the Madden-Julian Oscillation. Moreover there are uncertainties in the representation of clouds in the models (Randall *et al.*, 2007; Hegerl *et al.*, 2007). Each of the AOGCM has different uncertainties associated with them.

These AOGCMs are used in conjunction with future scenarios of change to predict future climate. The IPCC has come up with an approved set of scenarios described in the IPCC Special Report on Emission Scenarios (SRES; Nakicenovic *et al.*, 2000) These scenarios describe possible storylines in terms of future economic growth, technological development and social trends. There are four main storylines (Table 2.1) that result in a set of 40 scenarios (IPCC, 2001). Some studies still use the IS92 scenarios created by Leggett *et al.* (1992). These are a series of six emissions scenarios, which were changed in favour of the SRES storylines to provide an updated and a more complete picture of the uncertainties of future greenhouse gas emissions (Nakicenovic *et al.*, 2000).

Table 2.1: SRES Scenarios (Nakicenovic *et al.*, 2000).

A1	A global/economic narrative, with rapid economic growth and a global population that declines after a peak. New and efficient technologies are created. Different variants of this storyline depend on technological emphasis.
A2	A regional/economic narrative, in which countries evolve separately so that the global population and technology increase more slowly.
B1	A global/environmental narrative; like in A1 population grows rapidly before declining. However, in this scenario materialism reduces, clean and sustainable technologies are created and people work together. There is not, however, any additional climate legislation.
B2	A regional/environmental narrative where the world's dominant paradigm is one of local solutions and sustainability at all levels. Population growth and economic development is slow and technological development, though slow, is more diverse.

The way an AOCGM responds to changes from increased greenhouse gases (all external additions to the general climate system are termed 'external forcing') is characterised by two measures: the equilibrium climate sensitivity and the transient climate response. The equilibrium climate sensitivity is defined in the AR4 as "the equilibrium global mean surface temperature change experienced by the climate system following a doubling of atmospheric CO_2 concentration" (Randall *et al*., 2007, p.629). The transient climate response is the immediate response in annual global mean temperature at the time of CO_2 doubling (see Randall *et al* 2007). The AR4 AOGCMs cover a range of equilibrium climate sensitivity from 2.1°C to 4.4°C with a mean of 3.2°C (See table 8.2 in Randall *et al.*, 2007). Constraints from the observed climate

change suggest that equilibrium climate sensitivity may be between 2°C and 4.5°C supporting the AOCGMs simulations (Hegerl *et al.,* 2007). The range in climate sensitivities produced by the models is in part due to the differences in feedbacks from parameters in the models as well how each model deals with radiative forcing. This spread contributes to the range in projections (Randall *et al.,* 2007). The uncertainties in the climate change projections come from the models themselves, emission patterns of greenhouse gases and aerosols, and the internal climate variability (Hegerl *et al.,* 2007; Meehl *et al.,* 2007).

Europe

Projections by the IPCC (1998) indicate that winter temperature will rise by between 1.5-4.5°C all over Europe in the 21st century. However, this increase could be larger in boreal latitudes. Summer temperatures are also projected to rise though different models provide different results. The maximum projected rise is by 4.5°C (IPCC, 1998).

According to most IPCC models (IPCC, 1998; IPCC, 2001; Meehl *et al.,* 2007), precipitation is to increase in the high latitudes, possibly up to 20%, particularly in the winter months. In southern Europe, summer precipitation is expected to decrease substantially (IPCC, 2001).

Africa

Hulme *et al.* (2001) projected African climate to 2100 using a variety of emission scenarios and seven climate models, including HadCM2. They found that future annual warming across Africa ranged from under 0.2°C to over 0.5°C per decade and that warming was the greatest over the interior of the Sahara and central Africa. This is in agreement with IPCC models (2001), though the IPCC highlights the uncertainty in the magnitude of warming produced by various models. Recent models indicate an increase of 1.5-5°C mean annual temperature across Africa by the end of the 21st century (Meehl *et al.,* 2007).

Precipitation seems to be one of the hardest climate factors to model and accordingly Hulme *et al.* (2001), and the IPCC (2001) find an inconsistent signal in the direction and magnitude of change. Hulme *et al.* (2001) reported that none of the models used simulated multi-decadal rainfall regimes that are observed in the Sahel region. However, it is possible that newer models may correct this problem. Regional circulation models (RCMs) are much better at simulating rainfall patterns in the Sahel region because they can take into account factors at a

finer resolution. However, for the prediction of future climatic change AOGCMs are still needed because they provide the input for the boundary conditions in the RCMs (Huntley, pers. comm.). Nonetheless, current models project a decrease in rainfall in southern Africa and an increase in the rest of Africa, though with much variability (and uncertainty) throughout the seasons and areas (Hulme *et al.*, 2001; IPCC, 2001; Meehl *et al.*, 2007).

The projections of future climate change also show that the tropics and sub-tropics may experience climate with no modern analogue (Williams and Jackson, 2007; Williams *et al.*, 2007), which engenders difficulties when predicting species' responses.

2.1.4 Predicting Impacts of Climate Change

The predicted climate change may affect species on many levels: distribution, population size, biology, phenology and evolution (see above). Predicting impacts at these levels requires either the use of statistical models, where the outcomes are probabilistic due to the vast amount of uncertainty involved in projections into the future, or experiments. Predicting how species may evolve or micro-evolve in the future is near impossible. Hellmann and Pineda-Krch (2007) used a simple population genetic model to explore the effect of climate change on fitness using a hypothetical population under two scenarios of climate change: 1) a monotonically changing environment and 2) a periodic environment where amplitude and frequency of environmental extremes were altered. Under scenario 1, the population was able to track the changing environment closely with a decline in fitness depending on covariance between genetic traits. Under scenario 2, the population suffered a higher decline in fitness under greater environmental amplitude than under increased frequency of extremes. Studies into genetic variation and biological history may give an insight into past evolution and the scope for natural selection. Such studies have seldom been used in biodiversity conservation but offer a wealth of information (Willis *et al.*, 2007). The fossil record indicates few extinctions in the Quaternary period, which may be due to fast migration or adaptive evolution (Botkin *et al.*, 2007).

However, with future climate change projected to occur at a faster rate than ever experienced (IPCC, 2007) and the possibility of novel climates (Williams and Jackson, 2007), only experimental studies can truly give an idea of how species may adapt through evolution and phenotypic plasticity. Selection experiments, such as those done by Berthold and Helbig (1992), can give some indication of how species may change. Recent studies have found that some species can evolve increased dispersal rates through the success of more dispersive phenotypes

under climate change (Battisti *et al.*, 2006; Møller *et al.*, 2006; Pearman *et al.*, 2007; Thomas *et al*., 2001). However, simulations undertaken by de Mazancourt *et al.* (2008) showed that interactions with other species may inhibit evolution.

Gienapp *et al.* (2005) have recently developed a statistical tool to predict phenological change under climatic change. Their proportional hazards model was developed for predicting laying dates of *Parus major*. The model successfully predicted the expected effect of increased temperature on laying dates. Being probabilistic also meant that the effects of other factors, such as food availability or individual condition, could be included in the model (Gienapp *et al.*, 2005). This model is one of a kind and is likely to become useful as more studies follow suit.

Predicting how the biology of species may change, on the other hand, is difficult. Experiments exposing plants to increased CO_2 have given some insight into how species' biology and community dynamics may change (Graves and Reavey, 1996). However, these experiments only give an idea of what may happen if plants are suddenly exposed to vast quantities of CO_2 – an unrealistic scenario. These kinds of experiments are unethical to perform on animals and so observation or simulation models are necessary. Rodenhouse (1992), for instance, used a simulation model to predict the changes in the annual productivity of *Dendroica caerulescens* under projected climate change.

Estimating change in population size can be done using Population Viability Analyses (PVA) (Thuiller *et al.*, 2008; Wichmann *et al.*, 2005). McRae *et al.* (2008) developed an innovative framework to predict wildlife population trends. Their framework was three-fold. First, they simulated the effects of future land-use and climate change on vegetation using FORCLIM which is an individual-based forest dynamic simulator (Busing *et al.*, 2007). Second, they converted the resulting land cover data into habitat suitability maps for various species using expert opinion. These habitat suitability maps were then used along with climate change scenarios in the PATCH model, a spatially explicit individual-based animal population simulator that evaluates the outcome of species survival and reproduction, to estimate future mean population size. In their paper, they gave the results of an application of this framework that analysed and projected long-term (1990-2060) population trends for *Troglodytes troglodytes* and *Melospiza melodia*, two bird species residing in Oregon. They simulated initial population declines with later recovery in population size. Interestingly, they found that land-use change had a greater effect on species' survival than climate change. They also found that mean habitat suitability was a poor predictor of population change (relative to the 1990 values) as populations fluctuated more than mean habitat suitability (McRae *et al.*, 2008). In contrast to the poor link

between habitat suitability and population trends, Green *et al.* (2008) found a strong relationship between population trends and climate suitability. This indicates that the expert habitat suitability models created by McRae *et al.* (2008) may not be entirely valid.

The vast data requirements of PVAs often mean that extinction risk is usually inferred from the same models that predict change in distribution range under the assumption that range size is a good indicator of abundance. This assumption is not necessarily true as Shoo, Williams and Hero (2005a,b) demonstrate using empirical abundance patterns of endemic birds across an altitudinal gradient. Indeed, decline in population size can occur at a faster rate than the reduction in range size.

In the literature searched, no studies were found that looked at the impact of climate change on stopovers or the migration route of migrating species, though the basis for such studies already exists. Three studies provide the methodological basis upon which climate change impacts migratory species' stopover sites could be inferred. First, Farmer and Wiens (1999) used dynamic modelling to investigate migration strategies in terms of time spent at stopover sites and arrival at the breeding grounds. Second, Tankersley and Orvis (2003) combined maps of suitable stopover sites with flight algorithms to examine the importance of intact migratory routes for species survival. Third, Erni *et al.* (2003; 2005) created a simulation model of the migration of Palaearctic-African migrant birds to examine the survival rate along different migration routes, which included factors such as stopover sites.

There are numerous studies that have attempted to predict how species' distributions might change under global warming, which is mainly because the methodology is well developed. Peterson *et al.* (2001) summarise the methodological framework: 1) accumulation of large sets of present-day species' distribution; 2) the development of 'species distribution models' (SDM); 3) projecting regional shifts in geographic and ecological dimensions in the 'study area' based on the result of future scenarios GCMs; and 4) projecting fitted species-environment relationships onto the future landscape to obtain future distribution ranges. Guisan and Zimmermann (2000) define SDM as empirical models relating field observations to environmental predictor variables based on statistically or theoretically derived response surfaces. Species distribution models are, thus, basically a statistical characterisation of the species-environment relationship (Corsi *et al.*, 2000).

Data

Species data can be derived from expert opinion, observed presence/abundance obtained from surveys or museum collection, or presence and absence information obtained from extensive field studies. The first two types of data are the most easily acquired. Presence-absence data are difficult to obtain with any reliability. Indeed, true absences are hard to confirm. Failing to detect a species in the field does not necessarily mean that the species is absent. Assuming an absence, when a species is in fact present, results in omission errors (see below), which can lead to under prediction in a model, that is not predicting all areas where the species is actually present. Using presence-only data could be seen, therefore, as the only feasible course of action. Indeed in some cases it is. However, where available, reliable presence-absence data have been shown to be the most useful in predictive modelling (Brotons *et al.,* 2004) as such data allow for the description of a more discerning species-environment relationship. Data quality and quantity are important issues. Detailed data on species are often scarce, biased (in that samples are only taken near roads, rivers and easily accessible areas; Reddy and Dàvalos, 2003), and auto-correlated (Phillips *et al.,* 2004). Different modelling techniques address these problems differently and it is therefore important to use the correct method for the data available.

Sample size will also affect the accuracy of models (McPherson *et al*., 2004; Stockwell and Peterson, 2002). Data sets that are too small do not result in good models because a lot of the information on the species-environment relationship cannot be captured. Prevalence, which is the proportion of 'present' data points in the dataset, has also been shown to affect modelling techniques (McPherson *et al.,* 2004; Seoane *et al.,* 2005). Although this may be a data issue, it can also be an ecological issue: range size could be small resulting in few data points (Seoane *et al.,* 2005). Therefore it may be useful to consider the species' ecology before choosing the appropriate modelling method.

Guisan and Zimmermann (2000) suggest that there are three types of environmental variables that can be used as predictors in the species-environment relationship: direct, resource and indirect variables. Direct variables are those that impact directly on a species' ability to persist in an area, such as temperature and pH. Resource variables are those environmental factors that are required by the organism to live such as food, light and water. Indirect variables are those environmental factors, that are correlated with a species' distribution but which have no direct physiological significance like topography, geology, land-use and distance from roads (Austin, 2007; Guisan and Zimmermann, 2000). This classification is useful though a

simplification as some variables may be classified under more than one category. There is a fourth category, which modellers should be careful not to use, of spurious variables, i.e. those that correlate with a species' distribution but which have no meaning at all. Many studies use indirect variables for the construction of models because they correlate well with species' distribution (e.g. Austin *et al.,* 1996; Brotons *et al.,* 2004; Corsi *et al.*, 1999; Manel *et al.,* 1999; Zimmermann and Breitenmoser, 2002). However, in doing so the model loses its generality (applicability over different regions) and becomes only of local use (Austin, 2007; Guisan and Zimmermann, 2000; Zimmermann and Breitenmoser, 2002).

Several studies have advocated the use of climate variables as predictors of species' distribution (e.g. Beerling *et al.,* 1995; Gavin and Hu, 2005; Huntley *et al.,* 1995; Huntley *et al.,* 2004; Huntley *et al.,* 2007; Lees, 2002) as climate is a broad determiner of species' distribution – a direct ultimate factor (Root 1988a,b; Huntley *et al.,* 2007). This relationship between climate and species' distribution has been shown in many successful modelling studies (e.g. Huntley *et al.,* 2004). However, the sole use of climate variables for predicting species' distribution is determined by the scale, i.e. geographic extent and resolution, of the study. At fine scales, climate is too coarse to determine variation in species' distribution in which case other factors, such as land cover become important (Pearson and Dawson, 2003; Pearson *et al.*, 2004). Conversely, at coarse resolution, variables such as land cover become less useful (Thuiller *et al.*, 2004a). Two recent studies have demonstrated this. Luoto *et al.* (2007) investigated the importance of climate and land cover variables in bird SDM at four spatial scales. Land cover improved the climate models at 10 Km and 20 Km but showed no improvement at 40 Km and decreased model accuracy at 80 Km. However, they also pointed out that this finding was species dependant, with highly habitat-orientated species, e.g. the marshland bird *Circus aeruginosus,* having better fitting models that included relevant land cover variables. Heikkinen *et al.* (2007) investigated the role of biotic interactions in SDM. They found the predictive accuracy of models depended strongly on the spatial resolution: including biotic interactions was only useful at fine resolutions (10 Km).

The choice of direct and resource variables used has theoretical implications, because there would be some theoretical expectation or hypothesis about the shape of the response (Austin, 2007). This is often ignored in the choice of data or the formulation of the data model but has impact on the validity of a model (Austin, 2007; Rykiel, 1996). It has been shown that many of these direct variables' response curves follow a Gaussian-shaped curve (Austin, 2002, 2007).

Data for species and data for climate do not often cover the same area. It is therefore necessary to interpolate climate data to match the 'study area' for the species. It is important to examine this climate data because interpolations from poorly distributed meteorological stations can cause strongly auto-correlated climate surfaces. Meteorological station data are usually interpolated as a function of latitude, longitude and elevation. This can use observed data with variable coverage in space and time, or more uniform coverage and the climatic norm, i.e. 30 year average, which is usually 1961-1990, (Olwoch *et al.,* 2003). Olwoch *et al.* (2003) compared climate surfaces derived from these traditional data sets with purely process derived, modelled climate data and then looked at how these different data sets influenced simulated tick distributions. They found that 1) all three derived climate surfaces differed, 2) the simulated tick distributions were different using different climatic surfaces and 3) the modelled data set was equal to or slightly outperformed the traditionally interpolated climate surface in predicting tick distribution (Olwoch *et al.,* 2003). However, this new method will require further testing before more widespread use.

Models should be built using environmental/climate data and species data at similar scales to avoid prediction errors. Some mismatches in scale are unavoidable due to lack of data. Guisan and Thuiller (2005) argue that is the case in the use of GCM in future SDM as these climate models are built at scales much coarser than species data input to the SDM (Guisan and Thuiller 2005). Most SDM use fine scale climate data smoothed with the anomalies (difference between future prediction and the climatic norm), which resolves the issue of scale but carries the assumption that the fine scale pattern will not change in the future.

Species distribution models

There are many techniques that are used to formalise the species-environment relationship into SDM. Guisan and Zimmermann (2000) and Elith and Burgman (2003) provide good overviews of SDM. Table 2.2 provides examples of modelling techniques (the list is not exhaustive) that are used in conjunction with the three different types of species data. All techniques have their benefits and limitations (Brotons *et al.,* 2004; Zaniewski *et al.,* 2002). However, the method chosen for any particular analysis will depend 1) on the data available, 2) on the aims and objectives of the study, and 3) on scale of the study.

Table 2.2: Classification of species distribution modelling techniques (non-exhaustive list).

Species data	Techniques	Studies
Expert opinion	Multi-Criteria Decision-Making	Clevenger *et al.*, 2002; Doswald *et al*., 2007; Pereira and Duckenstein, 1993; Store and Kangas, 2001
Presence-only	Climate envelopes, Genetic Algorithm for Rule Set Protection, Maximum entropy, Ecological Niche Factor Analysis	Anderson *et al*., 2003; Beaumont *et al*., 2005; Farber and Kadmon, 2003; Hirzel *et al.*, 2002; Lees, 2002; Phillips *et al*., 2006; Phillips *et al.*, 2004; Zaniewski *et al.* 2002
Presence-absence	Generalised Liner Models, Generalised Additive Models, Climate Response Surface, Regression, Artificial Neural Networks, multivariate analysis	Augustin *et al*., 1996; Austin *et al.*, 1996; Beerling *et al.*, 1995; Corsi, *et al.* 1999; Doswald *et al.*, 2009; Gavin and Hu, 2005; Huntley *et al.*, 1995; Manel *et al.*, 1999; Thuiller *et al*., 2005

For the purpose of predicting the impacts of climate change on species' distributions, the scale of the study necessarily has to be large 1) because climate affects species on the macro-scale; 2) because GCM have coarse resolutions; and 3) to minimise projecting species' distributions into climate space different from that used to calibrate the model (Pearson *et al.*, 2004; Thuiller *et al.*, 2004b). For this type of modelling, techniques using expert opinion are not appropriate as climate has to be related to species' distribution by some statistical approach. Whether to use presence-only data or presence-absence data depends on what is available though it is generally accepted that presence-absence data provide the best results (Brotons *et al.*, 2004) because presence-only models provide overoptimistic predictions (Engler *et al*., 2004).

Kearny *et al.* (2008) used a mechanistic model, not using occurrence data, to model the distribution of *Bufo marinus* in Australia. Their model, using ecophysical data, is innovative but data intensive. This is the first geographic mechanistic model and, whilst the simulated distribution encompassed the range of the species, there was some over-prediction. The authors suggest that this approach could be used in conjunction with other methods (Kearny *et al.*, 2008).

There are many studies comparing different methods for modelling species' distributions (e.g. Araújo *et al.*, 2005; Elith *et al.*, 2006; Manel *et al.*, 1999; Meynard and Quinn, 2007; Leatherwick *et al.*, 2005). However, none of the studies are comprehensive and are rarely comparable (Austin, 2007). Nevertheless, these studies give an indication of the merits and

limitations of each method. Despite the rise of new methods, many new studies are falling back to using tried-and-tested methodology or using ensembles (Araújo and New, 2006).

Elith *et al.* (2006) found that some methods using presence-only data could provide useful predictions of species' distribution. They tested 16 different modelling techniques on a variety of data and found that those that were the most efficient (Maxent, multivariate regression splines and boosted decision trees) all had a high 'expressiveness' factor in the method, i.e. the technique could express complex relationships between the variables used (Elith *et al.,* 2006). Many authors using presence-absence data advocate that generalised regression techniques, such as Generalised Linear Models (GLM) and Generalised Additive models (GAM), and Neural Networks (ANN) provide the best SDM (e.g. Araújo *et al.,* 2005) and the analysis by Elith *et al.* (2006) also shows that they are good in presence-only modelling.

GAM and other non-parametric methods are generally preferred because they make fewer assumptions about variables. However, Huntley *et al.* (2007) argue that these techniques impose a shape to the species-environment relationship that may not be viable and seek global fits, which may cause interactions between variables to be missed. Climate envelope models (CEM) are another approach that has often been used. Most CEM can cope with presence-only data. However, they have many limitations. Most CEM cannot describe interactions between variables or show a varied suitability for the factors included in the envelope (Farber and Kadmon, 2003). Climate response surfaces (CRS), on the other hand, do not have these limitations although they cannot cope with presence-only data. CRS represent a multi-dimensional space comprising a particular combination of a range of values for environmental variables that describe a species' probability of occurrence in an area. CRS have been successfully used to model a number of species' distributions (Beerling *et al.,* 1995; Doswald *et al.,* 2009; Gavin and Hu, 2005; Huntley *et al.,* 1995; Huntley *et al.,* 2004; Huntley *et al.,* 2007). This non-parametric technique is particularly attractive for use in predicting species' distributions as it addresses species' responses to bioclimatic variables more specifically (so has a high 'expressiveness' factor) due to the use of locally weighted regression. Moreover, it allows interactions between variables and provides a response curve less smooth than other techniques, which reportedly allows for a better depiction of the realised niche (Austin, 2007; Huntley *et al.*, 1995).

The main critique of all these modelling techniques for predicting future species' distributions is fivefold. The first criticism has to do with the fact that the underlying assumption of all SDM is that species are in equilibrium with their environment (Guisan and Thuiller, 2005). This assumption is necessary because the species data input into the model is only a snapshot in

time. However, this assumption may not hold if the population was sampled when it was expanding or if it had been relegated to suboptimal habitat. Building models with such data will give a false representation of the species-environment relationship. Kearny *et al.* (2008) got over this problem by using a mechanistic model of the distribution of *Bufo marinus*, which is currently expanding its range in Australia.

The second criticism has to do with the concept of a species' niche (see Guisan and Thuiller, 2005). SDM, because they use observations of species, can only model species' realised niches, as species' current distributions will also reflect biotic interactions (Davis *et al.,* 1998; Guisan and Thuiller, 2005; Pearson and Dawson, 2003). Consequently, if interactions between species change as a result of climate change (as they have shown to do in the past; Davis and Shaw, 2001), predicted future distributions will be erroneous (Davis *et al.,* 1998). Best *et al.* (2007) showed with a simulation model, taking type of competition, density dependence and habitat fragmentation into account, that intra-specific competition would exacerbate the effect of climate change on species. Various studies have also shown that biotic interactions are very important in shaping species' current distributions and, consequently, limit the efficacy of SDM built with bioclimatic variables. Beale *et al.* (2008) set up a quantitative study to investigate how well species' distributions matched climate. They built a series of bioclimatic models and null models, first, using the distribution of bird species using observed data, then second, using synthetic data that was similar to the observed distributions but that were randomly placed with respect to climate. They then did a power analysis to determine if the distributions were determined by the climatic variables. They found that many of the null models performed as well, if not sometimes better, than the bioclimatic models. From this result and their power analysis they concluded that the birds' distributions in the study were not related to the climate variables used. They suggest that other factors may be (more) important and that biotic interactions could overwhelm the direct climate impacts (Beale *et al.*, 2008). Shuttle *et al.*'s (2007) experiment showed that, at a community-level, biotic interactions could overshadow the effects of climate change. Other studies, however, demonstrate that climate is still important in SDM. Costa *et al.* (2008) investigated which factors influenced species' distributions most (e.g. environment, inter-specific interactions, historical factors) by building SDM of closely related species across a steep longitudinal environmental gradient. Their results suggested that environmental variables clearly affected species' distributions but that competition and historical factors may also be involved. Duncan *et al.'s* (2009) revealing study agrees with this conclusion. Their study used data on the introduction of five South African dung beetle species to Australia. In the introduction

programme, the species released in Australia were selected by their climate compatibility, were raised in laboratory and released at sites where the primary resource was abundant. This ensured that the authors were confident that the confounding effects of dispersal limitation, resource limitation and natural enemies were removed, leaving climate as the determining factor. They then built SDM for 1) the Australian data with Australian climate, 2) South African data with South African climate and 3) for Australia projected from South African models. They found that the first set of models were the most accurate, whilst the second and third group of models were less good. They concluded that climate is important but that other constraints can limit model accuracy in some areas and for some species. However, their models were built on a very fine scale (10' x 10'), which would account for their results.

Third, most future SDM do not (properly) take dispersal into account (Guisan and Thuiller, 2005). The ability of species to disperse in the face of climate change (also ability to disperse in a fragmented landscape) will result in large differences in the impact climate change has on species (Davis *et al.*, 1998; Schwartz *et al.*, 2001; Thomas *et al.*, 2004b). Evidence from paleo-ecological studies show that species are likely to shift their ranges (Thuiller *et al.*, 2008) and so incorporating range shift, which is a result of fecundity, dispersal, recruitment and population growth (Massot *et al.*, 2008), into SDM is vital. Del Barrio *et al*. (2006) used an innovative integrated approach to investigate the localised effects of climate change. They used four modelling approaches: a continental-scale bioclimatic model, a regional bioclimatic and land-use model, a dispersal model (spatially explicit cellular automaton) and a connectivity model on two contrasting study regions. Their models revealed that many species would not be able to fulfil their potential future range.

Fourth, different modelling techniques result in different predictions of impacts of climate change, in terms of spatial extent and distribution (Thuiller, 2003, 2004), with no way of knowing which technique will be best for assessing future change. Thuiller (2004) suggests using different models and analysing consensus among models to help choose the best technique. Many of the differences found could be due to the different assumptions each SDM technique makes about the form of the species-environment relationship. If this is the case, then the CRS technique may be more reliable since it makes no formal assumption.

The final problem in current climate impact SDM modelling studies is the necessary coarseness of the models. Habitat alteration and loss impact immensely on biodiversity. However, inclusion of land cover variables at a coarse resolution is difficult because heterogeneity is lost (Thuiller *et al.*, 2004a; Luoto *et al.*, 2007). Pearson *et al.* (2004) developed a

hierarchical approach to circumvent the different resolutions between climate and land cover. Although this improved the SDM, not having data at the appropriate scales was limiting. Combining the effects of habitat loss and climate change and incorporating factors which impact on species' ability to persist, such as migration and ecological and evolutionary processes (Thuiller *et al*. 2008), will be a challenge in future modelling studies. SDM are also too coarse for conservation planning, though attempts are being made with the use of reserve selection algorithms (Araújo *et al.,* 2004). Despite these limitations, SDM are currently the best method available for assessing climate change impacts on species. Moreover, there is scope for improving SDM by including dispersal and population dynamic processes or biotic interactions (del Barrio *et al.,* 2006; Guisan and Thuiller, 2005; Heikkinen *et al*., 2007; Thuiller *et al.,* 2008).

Evaluation of species distribution models

Species distribution models are only useful if they provide an accurate picture of the 'truth', i.e. the models reflect the observations (good agreement between model predictions and input data). Oreskes *et al.* (1994) argue that the 'truth' of a model can never be demonstrated unless it is a model of a closed system. Therefore a model can only be evaluated. Many authors use the term validation interchangeably with evaluation. However, validation refers to a testing process that allows an assessment of how well the model performs and is only one component in model evaluation (Rykiel, 1996). Indeed, even if the model has minimal errors in terms of how it reflects the data used to calibrate the model (determined through validation) it does not necessarily follow that the model will perform well in a predictive sense (Oreskes *et al.,* 1994). There are thus two important components to model evaluation: testing how well the model fits the data used and testing how well the model performs in making predictions.

Testing how a model fits the data involves comparing the data used to build the model with the model predictions. The simplest way of doing this is resubstitution. However, this method overestimates the performance of a model due to over-fitting (Fielding, 2002). Bootstrapping (sampling with replacement), randomisation (sampling without replacement) and jack-knife sampling (leave-one-out method) are more robust in terms of evaluating the performance of a model (Fielding and Bell, 1997). All these methods suffer from not overcoming spatial and temporal autocorrelation, i.e. "the tendency of neighbouring sample units to possess similar characteristics" (Fielding and Bell, 1997, p.41) the result of which is that these methods overestimate a model's goodness of fit when extrapolated outside the remit of the training data

(Araújo *et al.,* 2005). The results of such methods should therefore not be used to infer a model's predictive ability. To test the predictive ability of a model, an independent data set, i.e. temporally and/or spatially independent, is needed. However, the availability or the feasibility of collecting such data is not always high. In such cases it is possible to partition the data collected so that one part is used to calibrate (train the model) and the other is used to test the model's performance. Most studies use a 70% partition of the data to build the model, the remainder being used to test it. While this method still does not avoid autocorrelation, it gives an indication of a model's predictive ability, albeit overoptimistic in comparison to using independent data (Araújo *et al.,* 2005).

Different techniques exist to validate the performance of a model and once again these depend on the type of data used to build the model. In presence/absence models, how well a model performs is usually determined through analysis of prediction errors. There are two types of errors that are characterised in an error (or confusion) matrix (Table 2.3): false positives (or commission error) where a species is predicted to be present where in fact it is absent (*b*), and false negatives (or omission error) where a species is predicted to be absent where it is in fact present (*c*).

Table 2.3: Error or confusion matrix (after Fielding and Bell 1997)

		Observations	
		present	absent
Model prediction	present	*a*	*b*
	absent	*c*	*d*

These errors do not carry equal cost in conservation. For instance, if the purpose of an SDM is to define areas for protection of a rare species, omission errors will be costly for the species. The values in the confusion matrix are obtained from a probability of occurrence model by placing a threshold on the probability. Different thresholds yield different values in the confusion matrix (Fielding and Bell, 1997). Often a threshold of 0.5 is used though there has been a move in recent studies to choose a threshold that maximises the accuracy of the model as measured by goodness-to-fit. Fielding and Bell (1997) give a good review of measures of goodness-of-fit. Kappa is one of the best threshold-dependent measures (Fielding and Bell, 1997; Manel *et al.*, 2001; Freeman *et al.*, 2008). Kappa has been shown to be sensitive to prevalence (Huntley *et al.,* 2004) though Manel *et al.* (2001) argue that this sensitivity to prevalence is slight compared with that of other measures derived from the confusion matrix (Fielding and Bell,

1997; Manel *et al.,* 2001). However, use of such threshold-dependent measures means that much of the information provided by the model is lost, and imposing a binomial system on a continuous variable can result in biases in the model output (Fielding and Bell, 1997). The receiver operating characteristic (ROC) plot is a threshold-independent measure that has been much used in medicine (Swets *et al.,* 2000). A ROC plot is obtained by plotting, for every threshold, the rate of true positives (y-axis called sensitivity) against the rate of false positives (x-axis called 1-specificity). The area under the curve (AUC) forms the index of model performance. The attainment of a straight line would signify a model performance no better than chance and an AUC of 0.5. Curves above that line with AUCs greater than 0.7 indicate good performance with values greater than 0.9 as excellent (Fielding, 2002; Swets *et al.,* 2000). Fielding (2002) advocates the use of ROC for evaluating presence/absence models. Moreover, AUC values are independent of prevalence (Manel *et al.,* 2001). However, Manel *et al.* (2001) argue that, although the AUC of a ROC plot is a good measure of a model's fit, it does not work when testing a model's predictive ability (by using an independent data set), because doing so "the model operation is no longer threshold independent" (Manel *et al.,* 2001). There are only a handful of studies that have validated their models with independent data sets (see Araújo *et al.,* 2005) and none have systematically tested the effects of different accuracy measures. As a consequence it is difficult to make decisions on the usefulness of such measures without more examination. Recently, a study by Lobo *et al.* (2008) criticised the use of AUC in predictive modelling. They highlighted five main problems. First, AUC is a discrimination index, i.e. "it represents the likelihood that a presence will have a higher predictive value than an absence" (Hosmer and Lemeshow, 2000, p.162), and does not necessarily measure the goodness-of-fit or accuracy of a model. Second, it equally weights omission and commission errors, which may be erroneous? However, most measures do this as well unless weights are used to correct this. Third, it measures the discrimination over all the information of the predictive model (though this is also its strength!). Fourth, it does not provide spatial distribution of errors. Fifth, it is influenced by prevalence, which makes it difficult to compare model performance between species with different prevalences. Most of these criticisms also apply to the other measures of goodness-of-fit. It is necessary to keep these in mind and not to abuse the use of any measure. However, as Lobo *et al.* (2008) do not provide any alternative to AUC, AUC is still useful as long as its limitations are realised and taken into account.

Validating presence-only built SDM is difficult because there are no absence data to compare with. Certain modelling techniques such as GARP get round this problem by generating

'pseudo-absences', which are obtained by randomly sampling a number of points for which there are no occurrences (Phillips *et al.,* 2004). The problem of this approach is that there is a great risk of omission error (Zaniewski *et al.,* 2002). Most presence-only modelling produces habitat suitability maps rather than probability of occurrence maps. Some studies have put thresholds to habitat suitability maps to yield presence-absence (Hirzel *et al.,* 2002). More innovative studies have used Spearman rank correlation between habitat selection/use by the species and habitat suitability as an indication of model performance (Boyce *et al.,* 2002; Doswald *et al.,* 2007). Ottaviani *et al.* (2004) propose two statistical methods for validating such models: 1) compositional analysis, where the overlap between presence data and habitat suitability is examined, followed by comparison to a null model, and 2) multinomial parametric bootstrap (for use with good quality validation data) in which validation is done using a generalised maximum likelihood type test. Validating presence-only models is a relatively new field in ecological modelling and therefore more research is needed to assess the validity of each approach.

Evaluating future climate SDM is difficult due to the uncertainty of how the climate will change. Most studies, using 'species-climate impact models', have only validated the fit of the current data to the simulated model (Araújo *et al.,* 2005). Some studies have used independent data sets in different regions (Beerling *et al.,* 1995; Duncan *et al.,* 2009), or have projected their models in the past and used fossil records (Martinez-Meyer *et al.,* 2004; Fløjgaard *et al.,* 2009). Projecting models into the past can be useful because it allows an examination of whether the actual observed range expansion or contraction of a species has occurred. However, it might be more useful if models could be built for past time periods then projected forwards to the present so as to capture the 'real' change in climate that is being observed. Such an undertaking would require good large-scale historic data for calibrating the models – an improbable task. Another possibility, though it would require a finer scale modelling, would be to model change in climate altitudinally as it has been shown that species are moving upwards in response to climate change (Sekercioglu *et al.,* 2008). Nevertheless, evaluating species-climate impact models is impossible due to unforeseeable factors (Araújo *et al.,* 2005; Oreskes *et al.,* 1994). It is thus important when building species-climate impact models to ensure the validity of the assumptions and the modelling methodology (Araújo *et al.,* 2005), and apply rigorous and critical evaluation of the projections. The modelling results should only be interpreted as giving an indication of the magnitude and direction of the probable impact of climate change. Thus current species-climate impact models are mainly strategic models, i.e. they give insight into key questions, rather than tactical models that give testable predictions.

Current predictions

Studies using species-climate impact models are not uniform in the species or areas they examine. Most studies use higher plants, butterflies or birds in Europe (often the UK), South Africa, Australia and North America. Geographic patchiness is due to data availability. These studies are varied in the use they make of such models, investigating not only species' future range changes, but also species' extinction risk or the effectiveness of protected areas. Thomas *et al.* (2004a) modelled the response to climate change in terms of distribution range of 1,103 endemic plant and animal species from around the globe. They then used the species-area relationship to estimate the extinction risk of species from climate change. Using two dispersal scenarios (full dispersal or no dispersal) and three climate scenarios for 2050, they projected that on average between 18% and 35% of species were committed to extinction. Many people have criticised this approach; in particular because of the use of the species area relationship (Hannah *et al.,* 2005) and, in general, because of the uncertainty associated with the methods used (Araújo *et al.,* 2005). Nonetheless their large-scale study highlighted the threat to biodiversity from climate change.

For Europe as a whole, the change in distribution under future climate scenarios has been modelled mainly for plants (Araújo *et al.,* 2004; Bakkenes *et al.,* 2002; Huntley *et al.,* 1995; Thuiller, 2003; Thuiller *et al.,* 2005a), birds (Huntley *et al.,* 2006; Huntley *et al.,* 2007) and butterflies (Hill *et al.,* 2002), as extensive data for these taxonomic groups exist. Huntley *et al.* (1995) used climate response surface modelling to simulate the potential future distribution of 8 higher plants in Europe under a double CO_2 climate change scenario. They found that many species showed marked shifts and reductions in potential future range. However, they stressed the uncertainties in the predictions they made. Indeed they highlighted that the marked changes simulated were unlikely to happen within the short time periods modelled and that there would probably be a mismatch between the latitudinal extent of the simulated range displacements and the photoperiodic requirements of the plants. In contrast to this careful use of the predictions made using uncertain climate change models, Bakkenes *et al.'s* (2002) study endeavoured to 'forecast' the effects of climate change on plant diversity and distribution by 2050. They stated that, on average, 32% of species would disappear from each grid cell (of Europe) and that, in 10% of Europe, species loss would be more than 25%, although 45% of Europe would have more species by 25%. Amongst these confusing percentages, however, they found that there was a general movement of species' ranges towards the North-east. This is in agreement with many

studies on range movement under climate change (e.g. Araújo *et al.,* 2004; Huntley *et al.,* 1995). They also found that species from drier southern areas would increase their ranges as they moved north and/or east, while, species from northern and eastern parts would be pushed out of their current range. This study, although interesting in many aspects, is problematic in the way it is reported, principally due to the lack of critical reflection of the methods used considering the uncertainty in predicting future outcomes. Huntley *et al.* (2007) also modelled the potential future distribution of all European breeding birds, using data from the EBCC Atlas (Hagemeijer and Blair, 1997). They found similar patterns to plants in that many species showed potentially substantial reductions in breeding range. Moreover, they found that only 39% of species' current range would still have a similar climate by 2100 (Huntley *et al.,* 2007). Similar patterns of range shift and reduction were found for 35 species of butterflies (Hill *et al.,* 2002).

For sub-Saharan Africa, McClean *et al.* (2005) studied the shift in climatically suitable areas for 5197 plant species for three future time periods (2025, 2055, 2085) using a climate envelope model and two genetic algorithm models. Dispersal was also taken into account though only a full dispersal scenario and a no dispersal scenario was used (two extreme and thus unlikely scenarios). Their models showed that between 81-97% of species' ranges decreased in size and shifted location (often to higher altitudes), whilst between 25-42% were projected to lose all climate suitability. Huntley *et al.* (2006) modelled the potential future ranges of sub-Saharan African breeding birds. They found a more complex pattern of potential change to that projected to occur in Europe. The distributions of species from South Africa, as well as those from semi-arid and eastern Africa, were projected to become more restricted, while those species associated with equatorial Africa and moist tropical forest habitat were projected to have relatively stable distributions. These two studies were the only ones found that looked at change in (non-invasive) species' distribution from a continental Africa perspective. The reason for this is probably the lack of good quality data for the whole of Africa (e.g. Giles, 2005). However, a number of studies have looked at climate change in South Africa. Erasmus *et al.* (2002) modelled the potential future range of 179 species in South Africa. They then superimposed on the future distributions, areas of the country that were currently transformed by human activity, as these areas would be effectively unsuitable for species' long term viability. They found that many species concentrated/retracted to the east (similar to the north-east shift in Europe) and that most species (139) also showed a range contraction. This eastward shift follows the current aridity gradient from east to west. However, the extent to which the eastward shift will occur in the future will also depend on the prevalence of standing water dispersed in the landscape from agriculture

(Erasmus *et al.,* 2002). In overlaying the anthropogenic landscape, Erasmus *et al.* (2002) highlighted the fact that there might be a conflict of land usage and suitability for species in the future. This was also demonstrated by Simmons *et al.* (2004) in their study on the impact of climate change on birds in South Africa. Indeed, the projected range shift of *Hirundo atrocaerulea* covered unsuitable human-impacted habitats so that projected future distribution of *Hirundo atrocaerulea* would be in reality much smaller. Their study also found that, on average, 40% of modelled birds' ranges would disappear by 2050. Although they cautioned that this percentage might increase when taking the anthropogenic landscape into consideration, modelling these species' ranges only in part of their geographic range (South Africa) may be misleading for the species as a whole. This problem does not arise when modelling endemic species. The impact of climate change and land use change on endemic Proteaceae, a plant family of great conservation importance in the Cape Floristic Region (CFR), was looked at in terms of future distribution, future Red List status (IUCN 2001) and effectiveness of the current and future protected areas (Bomhard *et al.,* 2005; Hannah *et al.,* 2005). In terms of effectiveness of current protected areas, Hannah *et al.* (2005) found that mountainous protected areas were useful due to the projected upwards movement of many species. Their study also found that species with small-range and, contrary to expectation, lowland species lost most range in the CFR because the climate is more uniform in the lowlands and so species require longer dispersal distances to find suitable habitat. Currently, the projected extinction risk of species from climate change is not included in the Red List assessment. Bomhard *et al.* (2005) used future climate scenarios and future land use change scenarios for 2020 (Rouget *et al.,* 2003) as well as the current and planned conservation areas to calculate the future Red List status of Proteaceae species. This novel way of using species climate impact models found that the current Red listing of species would not change much by 2020, though 29% of species modelled would be up-listed (i.e. to more threatened categories) when both land use and climate change were taken into account. Thuiller *et al.* (2006) also examined the future extinction risk of 277 mammal species using future distributions and current land transformations. Current land use was used since no future land predictions were available for Africa. They found that, under a full dispersal scenario, 39-50% of species would be classified as low risk by 2080 and, under a no dispersal scenario, between 25-35% would be classified as low risk (Thuiller *et al.,* 2006).

All the studies mentioned suffer from the limitations stated in the section on SDM. Moreover, none of these studies has evaluated their current SDM with independent data, an important step for future studies to take into account. Although many of these studies aim to

make definite predictions about the impacts of climate change at some future date, the future reality is unlikely to match such forecasts due to a number of factors. First, other factors than climate will affect species' distributions. Second, it is difficult to know how the anthropogenic landscape will interact with biodiversity. Third, some species may adapt to the new conditions and time lags to extinction will also confound factors. Fourth, as species respond individualistically to change, how communities will change or interact is difficult to conjecture. Nevertheless, all the current predictions for the change in species' distribution under climate change project similar patterns despite being modelled with different GCM, climate scenarios and modelling techniques. These models therefore provide us with a baseline of the direction and magnitude of change which can be improved upon by incorporating other factors into the models, such as better dispersal scenarios. Evaluation of these models will become paramount if their results are to be taken seriously by the wider public.

2.1.5 Conclusion

It is evident that climate is an important factor (amongst others) in many aspects of a bird's ecology. Changes due to global climate change have already been documented by a number of means and at a variety of levels, and as such are likely to continue to occur with increasing average temperatures and changes to precipitation patterns. Species distribution models are currently one of the most widespread tools for predicting the future effects of climate change on species' ranges. Regression-based non-parametric methods, such as GAM, are advocated as the best methods to use with presence-absence data. CRS is another non-parametric method, which shows promise but has not yet been rigorously compared with other methods. Furthermore, model robustness and transferability are issues that still need investigating. As discussed, all SDM techniques have a number of limitations, but they are one of the few tools available for examining the widespread impact of global warming on species' distribution. Therefore, thorough analyses of different SDM techniques need to form an integral first part of any study using these tools to investigate the impact of climate change on species.

Despite numerous studies implementing these models, none has specifically investigated the impact of the predicted change on migrant bird populations. The breeding ranges of all birds in Europe have been modelled in the present and the future (Huntley *et al.*, 2007). The non-breeding ranges of Palaearctic-African migrant birds have not yet been modelled with the

exception of *Acrocephalus griseldis* and *Emberiza cineracea* (Walter *et al.*, 2004) and *Acrocephalus paludicola* (Walther *et al.*, 2007). However, these studies' models are questionable. The simulated distributions greatly over predicted the species' actual distributions with the result that the authors clipped the simulated distribution with ecoregions that contained species' presence records. Thus, there is a great need to model current and future African non-breeding ranges of migrant birds.

Investigating the effects of climate change on migratory species is more complex than for non-migratory species. Not only do the changes in breeding and non-breeding ranges need to be examined, but also the changes along the migration route. Alongside issues of range expansion or contraction, are issues of changes to the length of the migratory pathway. This is important as changes in migratory distance may have implications for birds' fitness. Habitat availability/suitability also has to be considered along with species ecology. For instance, wetland areas are vital for some migrants, and change in these areas may exacerbate the effects of climate change. Moreover, a species' ecological characteristics may help identify those species most vulnerable to climate change.

The possibility of phenological miscuing and disjunction is greater in long-distance migrants as there is an indication that photoperiod is a prime cue for departure from the non-breeding grounds (Kok *et al.*, 1991; Coppack *et al.*, 2003). This may exert a selection pressure on migrants to select different non-breeding grounds. Examining the potential effects of climate change on the migratory strategy of each species might give an indication of species' plasticity. It is expected that partial migrants, such as *Sylvia atricapilla*, will adapt more easily to climate change due to their ability to change migratory behaviour. Competition between resident, short-distance migrants and long-distance migrants may also change under climate change if short-distance migrants start to overwinter on the breeding grounds. It will therefore be of interest to investigate community turnover of migratory birds.

Notwithstanding the problems associated with species-climate impact models, such as data availability, model choice and evaluation; migrant populations provide further complications for studying the effects of climate change, as change in populations may be the result of changes on the breeding grounds, non-breeding grounds or combination of both. Examining past population changes will be necessary so that a comprehensive perspective on the potential effects of climate change on can emerge. In order to arrive at an accurate picture of the effects of environmental change on Palaearctic-African migrant birds, it will be necessary to model past, present and future climate suitability.

2.2 Aims and Research Questions

1) Model the present distribution of Afro-Palaearctic migrant birds on their breeding and non-breeding grounds.
   a) How does model selection affect robustness and predictive ability?
   b) Are there differences between modelling methods?
   c) Can good species distribution models be constructed for the breeding and non-breeding ranges of migratory birds?
   d) What affects the performance of species distribution models?

2) Project the distribution of Afro-Palaearctic migrant birds into three future time frames: 2025, 2055 and 2085.
   a) Do comparable modelling methods produce different future projections, i.e. what is the uncertainty surrounding future projections?
   b) How will the projected climate change affect migratory birds?
   c) Are there differences among migratory groups?
   d) Will climate change impact on species migratory behaviour?

3) Assess the vulnerability of species to climate change.
   a) What factors impact on species vulnerability?
   b) Which species are most vulnerable to climate change?
   c) How much can be inferred from SDMs in terms of population changes?
   d) Is there any relation between past population change and projected future risk?

3. Modelling the breeding and non-breeding ranges of European-breeding migratory birds

Species' distributions in time and space are fascinating to biogeographers and ecologists alike. To study these macro-phenomena, the concept of niche was developed. Grinnell (1917), Elton (1927) and Hutchinson (1957) were all pioneers in the concept of niche, which is broadly defined as a place where a species can potentially live (Grinnell, 1917) or a species' place in the biotic environment in terms of its ecological function (Elton, 1927). Hutchinson refined these theories of niche by introducing the concepts of fundamental and realised niche (Hutchinson, 1957). The fundamental niche refers to the area in environmental space (comprising conditions and resources) where a species can live (a definition with similarities to that of the Grinnellian niche; Pulliam, 2000; Soberon, 2007), whereas the realised niche is the area within the fundamental niche that the species actually occupies as a result of biotic interactions (a definition with similarities to the Eltonian concept of niche (Soberon, 2007)). These concepts are crucial to the study of species' distributions. Indeed, the n-dimensional niche described by Hutchinson provides a framework for modelling species' distributions.

Before introducing the conceptual framework of species' distribution modelling, it is vital to define properly certain terms that will be used throughout this work. Certain terminology has been much debated or left unexplained (Corsi *et al.*, 2000; Kearney, 2006; Scott *et al.*, 2002), hence the need to state explicitly how each term is used.

Species' distribution refers to the geographical distribution of species' occurrence. Species' distribution and range are used interchangeably here. Habitat is defined as "a description of a physical place, at a particular scale of space and time" (Kearney, 2006, p.186). A model is a simplification of a biological system. Species distribution models (SDM) relate a species' distribution (response variable) to environmental variables (predictor variables). However, here I break down this definition to two parts: a set of environmental variables that describe a species' distribution (conceptual model) and the statistical procedure (modelling method) which relates the environmental variables to species' distributions.

SDM are developed by intersecting observed data with predictor variables (see Chapter 2) that are thought to encompass a species' niche. But which niche? Because observed data are used, SDM cannot represent a species' fundamental niche (Kearney, 2006; Pearman *et al.*, 2007). However, whether SDM really model a species' realised niche (the

definition used by most modellers) is also questionable since biotic interactions are not directly input into the model (Martinez-Meyer, 2005) and this assumption is rarely investigated. However, predictor variables that represent biotic interactions have been successfully included in models with realised niche concepts (Anderson, Peterson and Gomez-Laverde, 2002; Heikkinen *et al.*, 2007). Many authors advocate the use of niche in terms of potential habitats for species' distribution (Araújo and Guisan, 2006; Kearney, 2006). In this vein, I will refer to niche as the climatic space where a species can potentially live because of the purpose of the models (effect of climatic change on species) and the coarse scale of the models used in this study (Kearney, 2006; Soberon, 2007). Scale is an important consideration when developing SDM (see Chapter 2) since the scale partly determines the model and hence the predictor variables.

Determining a set of predictor variables and selecting them for the migratory birds' distribution models forms the basis of the next section (Section 3.1). The choice of predictor variables is determined by the relationship sought and the scale of the study. At the local scale, landscape heterogeneity will influence species' distributions more than at an extensive scale (Pearson *et al.*, 2004). On a coarse scale, macro-phenomena like climate are likely to be more important. An initial selection of predictor variables is made on the basis of expert judgement/review of the relevant literature. The final choice of predictor variables and their interactions is then made through different methods: either *a priori* or through variable selection methods (see section 3.1). A recent study by Meynard and Quinn (2007) found that an expert-based variable selection performed better than the traditional automated procedures. They tested different statistical models and associated variable selection on artificial species and found that many methods did not pick the 'true' environmental variables. Selecting environmental predictors for a predictive model is complicated by the fact that there is a need to regularise the models, i.e. balance model fit with model complexity (Reineking and Schroder, 2006; Thuiller *et al.*, 2008). Therefore, one cannot just 'throw' all seemingly important variables into a model. Issues of over-fitting and generality in reference to predictive models are discussed in Section 3.1.

Choosing an appropriate method for modelling the distribution of migratory birds forms the basis of section 3.2. The response variable available (as well as the potential relationship between the response and the predictor variables) will determine which methods can potentially be used (see Chapter 2). However, how good the data are is also important to consider. Species' recorded presences/absences are often biased and will necessarily contain errors (see Chapter 2). The data that we have for this study includes bias and error. Indeed, although occurrence data for the breeding grounds are relatively good, there is more

uncertainty about the whole validity of data for the non-breeding grounds. Graham *et al.* (2007) investigated the influence of spatial errors in species' occurrence data on the performance of SDMs. They found that the regression methods, such as GAM, were robust to spatial errors and model performance did not decline as a result. Regression methods have also increasingly been found to be some of the best modelling methods for predictive species distribution modelling (Elith *et al.*, 2006; Graham *et al.*, 2007; Guisan *et al.*, 2007; Meynard and Quinn, 2007; Randin *et al.*, 2006). The choice of modelling technique is closely related to the objective and therefore there is no single 'best' method (Van Horne, 2002). However, since my goal is prediction, it is paramount that the models do not over-fit the data and that they are robust.

Section 3.3 of this chapter presents the resultant models for the breeding and non-breeding ranges of European-breeding migrant birds. The models are the culmination of the analyses in sections 3.1 and 3.2. The models relate species' observed distributions to climatic predictor variables. This creates inevitable discrepancies between the observed and simulated data. Prediction errors such as these are inevitable in SDM (Barry and Elith, 2006). Section 3.3 examines the sources of uncertainty and the limitations of the models.

3.1 Species distribution models: variable selection

3.1.1 Introduction

The conceptual framework and the statistical formulation of species distribution models (SDM) are already well formed (Guisan and Zimmermann, 2000). However, choosing an appropriate model still seems to cause modellers difficulty, especially when the model outputs, often fraught with uncertainty, are to serve as arguments for policy makers. Models are never accurate depictions of the real world but can reflect well the data used to build the models. However, how 'well' is judged depends on various criteria according to the many authors that have built SDM (Araújo *et al.*, 2005; Flather and King, 1992; Huntley *et al.*, 2004; Manel *et al.*, 2001; Thuiller, 2004; Thuiller *et al.*, 2005). The initial steps to building a model, which are often overlooked in studies today, are to state 1) what purpose the model has, 2) what criteria make the model acceptable to use and 3) in what context the model is intended to operate (Rykiel, 1996). It is fulfilment of these factors that will determine whether or not a model performs 'well'. There currently exist many 'proven' techniques for modelling species' distribution (Elith *et al.*, 2006; Guisan *et al.*, 2002; Thuiller, 2003). The choice of dependent variables to incorporate into the model will depend on the purpose of the model and the scale of the data.

Fielding (2002) urges modellers, when developing SDM, to consider statistical issues such as parameter estimation and model specification as well as pragmatic issues such as accuracy, generality, complexity and cost (monetary and computationally). These issues are involved in complicated trade-offs; for example, if the model form is too complex it loses generality but if it is too simple it loses accuracy. As in the case of classification errors (commission versus omission errors, see Fielding 2002), the cost of generality and accuracy depend on the purpose of the model.

The purpose of most SDM is prediction; whether to predict where a species currently is, based on relatively few occurrence points, or to predict where a species' range might lie under some future scenario.

Most modellers agree that for a model to be acceptable for use, it has to be 'validated'. What most authors mean by validation is what Rykiel (1996) calls operational validation where simulated data are compared to observational data. Operational validation, however, is but part of validation, which is defined as "a demonstration that a model within its domain of applicability possess a satisfactory range of accuracy consistent with the intended application

of the model" (Rykiel, 1996, p.233). Conceptual validity, where "the theories and assumptions underlying the conceptual model are correct, or at least justifiable, and that the model representation of the problem or system, its structure, logic, mathematical and causal relationships, are recognisable", is just as important (Rykiel, 1996, p.234). This means that the model chosen to represent species' distribution needs to be ecologically valid. Conceptual validity is not often considered as the many variables included in SDM shows (Bakkenes, 2002; Corsi, 1999). However, neither operational validity nor conceptual validity in themselves necessarily show that a model is any good at predicting. Indeed, a high concordance between simulated and observed data may arise because the model over-fits the data (Fielding, 2002).

Although many agree that, in terms of testing how well a model predicts, an independent data set should be used, most do not do so through an understandable lack of data. The next best things are data splitting methods, although many authors have not used these techniques (see Araújo *et al.*, 2005). The main problem with these methods is autocorrelation (Araújo *et al.*, 2005; Fielding and Bell, 1997). Araújo *et al.* (2005) attempted to determine 1) how well models performed on independent data sets; 2) whether using partitioning methods (fitting the data to a randomly selected 70% of the data and testing it on the remaining 30%) were good surrogates for accuracy on independent data; and 3) whether any modelling technique was any better than the others. They used four modelling techniques and variables were chosen through a stepwise procedure using Akaike's information criterion (AIC). Operational validity was tested using Cohen's Kappa and the area under the curve (AUC) of a receiver operating characteristic plot (Fielding and Bell, 1997). They reported first, that models' predictive accuracy was quite good; second, that validation on non-independent data produced overoptimistic results; and third, that some techniques (Generalised Additive Models and Artificial Neural Networks) were consistently best. However, this study only tested the viability of one model using each technique discarding the environmental variables early on through AIC. Each combination of variables constitutes a model and the relationship between AIC, AUC and prediction is not well understood. Model selection and model validation is a circular process with the selection of variables a central step (Araújo and Guisan, 2006). Further, randomly selecting 70% of the data for fitting the model just the once leaves the possibility that the result may not be representative. Fitting the model several times to different randomly selected 70% data sub-sets is required to assess the reliability and the robustness of a model.

Many studies have compared techniques for relating variables to species' distributions, but not many have compared how variable selection can affect model validity.

Moreover, validity is rarely fully investigated leaving seemingly good models in use when they are in fact problematic for their intended use. Here I investigate these issues in the context of developing models for the breeding and non-breeding ranges of Afro-Palaearctic migrant birds. These models are built with the purpose of predicting the change in distribution of these species under climate change. They need to be able to predict future range change and so be capable of extrapolating. Therefore, they must not be overly simple whilst retaining some degree of generality. The models consequently need to be able to simulate robustly the species' current distribution and be based on sound theory.

Predictor variables

Good biogeographical models require a strong link between ecological theory and statistical models (Guisan *et al.*, 2006). It is important to incorporate meaningful predictor variables in tune with the scale and purpose of the model and express and relate these in such a way that they adequately reproduce species' responses to these variables. Bioclimatic variables are ultimate factors constraining a species' distribution on a coarse scale (Root, 1988a,b; H-Acevedo and Currie, 2003; Huntley *et al.*, 1995; Lemoine and Böhning-Gaese, 2003). Moreover, they have been shown to approximate a variety of species' distributions very well (Huntley *et al.*, 2004). This is because bioclimatic variables affect species directly, for instance by imposing physiological limits (temperature), as well as indirectly. This fact and the fact that climate models (AOGCMs) and emission scenarios (see Chapter 2) are available to use, are why using bioclimatic variables (instead of other variables for which predictions of future change are lacking) are at the same time the best option and problematic. Problematic because the variables may not describe the entire species-environment relationship, especially if species' realised niche is constrained by biotic factors. Future predictions may therefore be uncertain because a realised niche may be different under different climates and also because there is no information on how species may respond to novel climates. However, the use of bioclimatic variables is currently the most viable option.

It has been shown that many direct variables such as bioclimatic variables often commonly produce unimodal-skewed responses in ecology (Austin, 2007; Austin, 2002), which non- or semi-parametric methods reproduce well (Guisan *et al.*, 2006). Therefore techniques, such as Generalised Additive Models (GAM) or Climate Response Surfaces (CRS), are and have been shown to be viable methods for predictive biogeographical modelling (See Chapter 2).

Having decided on a viable technique and the broad category of variables to use, the questions then become which variables will give the best model and how do these variables relate to the response variable, i.e. singly or through interactions? Guisan and Thuiller (2005) urge us to consider interaction terms when building SDM as they often improve model fit.

Although it is possible to try every possible combination of variables in a model, this course of action is not sensible. First we must come up with a set of candidate models that we think approximates the reality given the data at hand. These models should be based on sound ecological theory and when possible on previous studies. The best model(s) (and combination of variables) should then be chosen by a valid technique and then the model examined to establish whether it makes ultimate sense through a goodness-of-fit test (Burnham and Anderson, 2001).

Model selection

Choosing an appropriate model in ecology has been done in the past through hypothesis testing, e.g. variables selected by stepwise regression (Mazerolle, 2004). However, it has been argued that this is not the best way of selecting models because it has a number of drawbacks; for example, stepwise regression methods can lead to biases in parameter estimation and the final model selected changes depending on how the regression is operated (Burnham and Anderson, 2001; Johnson and Omland, 2004; Wittingham *et al.* 2006). In recent years there has been a move towards using information-theoretic approaches, especially the Kullback-Leibler information statistic (K-L) as a basis for making strong inferences in ecology (Burnham and Anderson, 2001).

The information-theoretic paradigm is partially based on four core principles in science: 1) there are no true models, 2) the best models are simple and parsimonious, 3) there exist at first several working hypotheses and 4) the best models are found through the strength of evidence they provide (Burnham and Anderson, 2001). The relationship between K-L and maximum likelihood forms the basis for Akaike's information criterion (AIC; Eq. 3.1) which has become one of the best tools for model selection in ecology (Burnham and Anderson, 2002).

$$AIC = -2\log(L(\hat{\theta} \mid data)) + 2K \qquad (3.1)$$

Where $(L(\hat{\theta} \mid data))$ is the value of the log-likelihood at its maximum point over the unknown parameters θ, given the data and K is the number of estimable parameters in the model (Burnham and Anderson, 2001, 2002).

AIC is essentially an estimate of the expected relative loss of information when a model approximates reality (fitted model versus observed data). By minimising AIC, we minimise the loss of information and select the model (with the lowest AIC) that is closest to the 'truth' (Burnham and Anderson, 2002). Moreover, AIC takes into account the number of parameters in the model and promotes parsimony. Burnham and Anderson (2002) point out that if only poor models are evaluated then AIC will only select the best out of a poor selection. Further, the absolute size of the AIC is meaningless, the relative values over all models considered being what is important. AIC values are compared between models most simply and effectively by taking the difference between each model and the best model (Δ AIC; Eq. 3.2):

$$\Delta_i = AIC_i - AIC_{min} \tag{3.2}$$

The larger theΔ of model i, the less plausible a model and the rule of thumb suggested by Burnham and Anderson (2002) is thatΔ_i values between 0-2 provide substantial evidence in favour of that model, values between 4-7 provide less support for that model and values over 10 provide essentially no support for that model.

In the field of species' distribution modelling where the response variable is binomial, goodness-of-fit measures (which assess the prediction errors of a model) have often been used as a support for a model. The main goodness-of-fit measures used are Cohen's Kappa (Eq. 3.3; Cohen, 1960) and the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding, 2002; Fielding and Bell, 1997; Zweig and Cambpell, 1993).

$$K = \frac{(a+d) - (((a+c)\times(a+b)) + ((b+d)\times(c+d)))}{1 - (((a+c)\times(a+b)) + ((b+d)\times(c+d)))} \tag{3.3}$$

Where a represents correctly predicted presences, c incorrectly predicted presence, b correctly predicted absences and d incorrectly predicted absences.

Goodness-of-fit measures are based on the two types of errors that are characterised in an error (or confusion) matrix (Table 2.3). Cohen's Kappa evaluates not only how well a model performs in terms of correct proportion of presence and absences (Table 2.3) but also the extent to which the model performs better than random. However, as discussed in Chapter 2, Kappa (K) is a threshold dependent measure which may cause a loss of information when assessing the goodness-of-fit of a model (Fielding, 2002; Fielding and Bell, 1997), therefore AUC, which is threshold independent, is considered a better alternative when it comes to evaluating the performance of a model. A ROC plot (Fig. 3.1) is obtained by plotting, for

every threshold, the rate of true positives (y-axis called sensitivity) against the rate of false positives (x-axis called 1-specificity). The area under the curve (AUC) forms the index of model performance. A straight line would signify a model performance no better than chance and an AUC of 0.5. Curves above that line with AUCs > than 0.7 indicate good performance with values > 0.9 as excellent (Swets, 1988). Both K and AUC have had criticism levelled at them (see section 2.1.4). However, they are still the main measures of model performance currently being used. Therefore, their deficiencies will be taken into account in the reporting of any results.

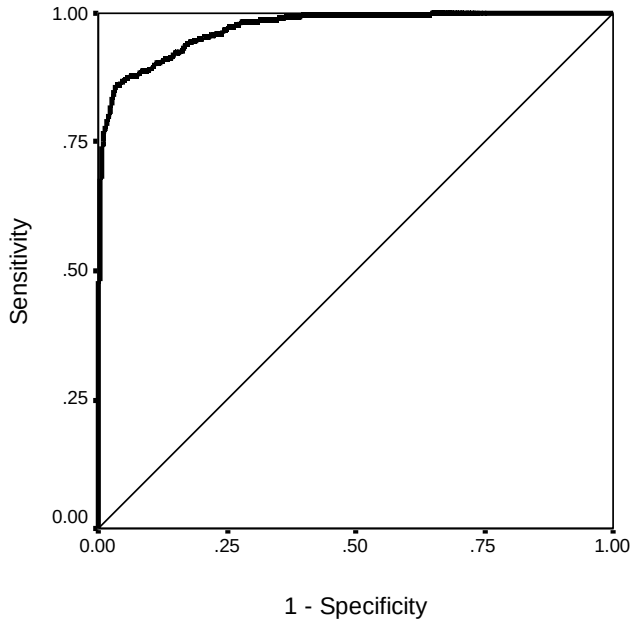


Figure 3.1: ROC curve for *Troglodytes troglodytes* for model 7i (see Table 3.2) with an AUC value of 0.971. The thin straight line represents the mid section under which the area would be 0.5.

Goodness-of-fit measures are normally used for evaluation of models (last step of model formulation) rather than model selection. These measures evaluate the predictive capability (when used in conjunction with cross-validation techniques) of a model and do not take things like parsimony into account. It is important therefore to examine the relationship between typical model selection measures such as AIC and model evaluation measures such as AUC.

In this section, I will look at the relationship between AIC and AUC, and examine model complexity and robustness through resubstitution and data-splitting methods using Generalised Additive Models. I will then examine the effects on prediction through projecting a portion of the data onto future climates and onto an independent data set. These results will form the basis for selecting the best combination of variables for migratory birds.

3.1.2 Methods

Species data

Extent of occurrence data for the breeding and non-breeding ranges of 229 migrant birds (Table 3.15) were taken from BirdLife International (BirdLife International, 2010). They were in the form of shapefiles in a Geographic Information System's database. The original data had come from various sources, but had been assembled and corrected by ornithological experts. These shapefiles were subsequently gridded to a 0.5 degree grid over Europe and North Africa and to a 1 degree grid for sub-Saharan Africa (including Madagascar). Sub-Saharan Africa was gridded to 1 degree to allow for uncertainties (Guisan *et al.*, 2007) in range margins in some regions of sub-Saharan Africa. European breeding data were also taken from the European Bird Census Council (EBCC) atlas (Hagemeijer and Blair, 1997) as these better quality data were also available. These latter data were available on a 50 x 50 km Universal Transverse Mercator (UTM) grid. The area considered in this thesis comprised the Western Palaearctic, as defined by Snow and Perrins (1998), as well as Africa, Madagascar and the Cape Verde Islands. The taxonomy used was the same as that used in Snow and Perrins (1998).

To test the effects of the different model selection techniques on prediction, the breeding ranges of 12 Palaearctic migrant birds were selected so that widespread and range-restricted species (species with prevalence ≤ 0.1) were represented with passerine s, birds of prey and wader groups (Table 3.1). Within these groups a total of 12 species were randomly chosen. The number of species selected was the minimum adequate number for this analysis. Less would not have been viable and more, although desirable, would have been time costly and outside the scope of the thesis, which was mainly concerned with predicting general impacts of climate change on species rather than with an in depth methodological study. Species' lists from European Important Bird Areas (IBA) were taken from BirdLife International's World Bird Database. There were 1503 sites which contained presence absence information for the twelve species. The resolution of these points was one degree.

Table 3.1: Selection of species (^{W} indicates the widespread species) and observed prevalence (proportion occupied) on the breeding grounds.

Family	Species	Common name	Prevalence
Accipitridae	*Accipiter nisus*^{w}	Sparrow hawk	0.38
Accipitridae	*Gyps fulvus*	Griffon vulture	0.10
Accipitridae	*Pernis apivorus*^{w}	Honey Buzzard	0.28
Caprimulgidae	*Caprimulgus ruficollis*	Red-necked nightjar	0.05
Charadriidae	*Charadrius morinellus*	Dotterel	0.03
Hirundinidae	*Hirundo rustica*^{w}	Swallow	0.55
Laniidae	*Lanius nubicus*	Masked shrike	0.03
Rallidae	*Porzana porzana*^{w}	Spotted crake	0.17
Scolopacidae	*Actitis hypoleucos*^{w}	Common sandpiper	0.32
Scolopacidae	*Limosa lapponica*	Bar-tailed godwit	0.01
Sylviidae	*Sylvia communis*^{w}	Whitethroat	0.41
Sylviidae	*Sylvia undata*	Dartford warbler	0.09

Climatic data

Climatic data for the period 1961-90 were taken from the 0.5º longitude x latitude global compilation of New *et al.* (1999). Soil water capacity data were taken from Prentice *et al.* (1992). These data were interpolated for our study area, which comprised 10313 grid cells for the non-breeding distribution and 8233 grid cells for the breeding distribution (Europe and North Africa only unless species also bred south of the Sahara[1]), and also to the 1503 grid cells for the IBA data set, using an inverse distance weighted bi-linear interpolation (see algorithm in Numerical Recipes Software, 1988-1992[2]). A series of bioclimatic variables was derived from the climatic variables (see Huntley *et al.* 1995 and Prentice *et al.* 1992 for the calculation of these variables). These were the annual temperature sum above 5ºC (GDD5), which is the minimum temperature for tree growth (Prentice *et al.* 1992), the mean temperature of the coldest month (MTCO), the mean temperature of the warmest month (MTWA), actual/potential evapo-transpiration (APET), difference of precipitation to potential evapo-transpiration (PPE) and a dry intensity variable (DRYINT) which is formed by taking the negative values of PPE. PPE was divided into three variables: annual mean PPE, PPE during the breeding/non-breeding season and PPE during the two months prior to the

[1] 44 species also breed in Sub-Saharan Africa (see digital appendix). For these species, the entire study area (10313 cells) was used to build the breeding models.

[2] In the case where the target cell did not have 4 corner points (e.g. because it was coastal),a window was placed around the point and the inverse distance weighted mean using all the data points falling within the window was calculated. The weights given to the points within the window were 1/(distance from target point), so points further away got a lower weighting than points closer to the target point.

breeding/non-breeding season (see below). PPE was transformed due to the very large values at northern latitudes (a result due high wetness and low evapotranspiration). Transformation was done by ranking the values then taking the percentile.

The future climate (derived from the HadCM3 general climate model and the B2 SRES scenario) for the study area was interpolated from the TYN SC 2.0 0.5º longitude x latitude global compilation by Mitchell *et al.* (2004). This data set provides future climate variables derived by adding the climate anomalies for 2070-2099 to the 1961-1990 climate values (Mitchell *et al.*, 2004).

Models

Huntley *et al.* (2004) showed that a variety of species' distributions could be very well modelled using just a few bioclimatic variables. This is because these base variables characterise the environment in which the species live. The base model from Huntley *et al.* (2004) is GDD5, MTCO and APET. In another study modelling bird distributions in Africa, MTWA was used instead of GDD5 because it was deemed and found to be a better variable for Africa (Huntley *et al.*, 2006). These two 3-variable combinations formed the base for all the models used (Table 3.2). Models comprising of less than these 3 variables (termed 'simple models') were also tested (though only on the selected 12 species) using these core variables including a null model which was each species' prevalence. Models with more than four variables were never tried because the variables are already correlated (significant Pearson correlations from 0.135 to 0.918). Abiotic interactions were taken into account by running the main models two times – no interaction and interaction: temperature (MTCO or MTWA) and APET.

Since migrant species spend limited amounts of time in each region (breeding and non-breeding) it makes sense to 'fine tune' some of the variables rather than using annual means. Heikkinen *et al.* (2006) found that models incorporating fine-tuned variables performed better than the base line models. However, they studied a relatively fine-scale (10 x10 km grid) while I used a half degree grid. It makes no sense, therefore, to fine tune all of the variables because, at a coarse scale, an environment in which the species lives is characterised by the climate over the year. PPE was chosen as the fine-tuneable variable. Moisture variables were deemed especially important for species during the time they were in each region, for determining food abundance for instance. Temperature was not considered

for fine-tuning because 1) it is important in the base line variable[3] and 2) another temperature variable would be too highly correlated in the model. I considered it would be worth building models with variables adjusted to the period birds were in each region and also to a period shortly before the birds' arrival. The before period was taken as two months before arrival. Arrival time in each region is difficult to estimate because all species have different arrival times and populations arrive in different parts of the region at different times. Moreover, due to the coarse scale of the modelling, a generic arrival time was used. The two months before arrival were considered for the breeding range as February-March and September-October for the non-breeding range. The "breeding period" was defined as April-August and the "non-breeding period" as October-February.

Table 3.2: Main models tested (MTCO= mean temperature of the coldest month; MTWA=mean temperature of the warmest month; GDD5=growing degree days over 5ºC; APET= actual/potential evapo-transpiration; PPE= difference of precipitation to potential evapo-transpiration; PPE_{BEFORE}=PPE before breeding or non-breeding season; PPE_{DURING}=PPE during breeding or non-breeding season; DRYINT=dry intensity variable). See appendix IIIa for the list of reduced models used for the 12 species.

Model N°	Model
1	MTCO + MTWA+ APET
2	MTCO + GDD5+ APET
3	MTCO + MTWA+ APET + DRYINT
4	MTCO + GDD5+ APET + DRYINT
5	MTCO + MTWA+ APET + PPE
6	MTCO + GDD5+ APET+ PPE
7	MTCO + MTWA+ APET + PPE_{BEFORE}
8	MTCO + GDD5+ APET + PPE_{BEFORE}
9	MTCO + MTWA+ APET + PPE_{DURING}
10	MTCO + GDD5+ APET + PPE_{DURING}
N°i	Model + (MTCO*APET)+(MTWA/GDD5*APET)

Modelling technique

Generalised additive models (GAM) are semi-parametric models with the assumption that the functions are additive and the components are smooth (Hastie and Tibshirani, 1990), i.e. a function is created that captures the pattern in the data whilst eliminating the noise. The models make no assumption about the form of the relationship between the response variable and the predictor variables, and therefore is data-driven (Guisan *et al.*, 2002). This technique aims to maximise the quality of prediction by estimating non-parametric functions of predictor variables. GAM are generalisations of the additive models (Eq. 3.5) which in turn are generalisations of linear regression. GAM (Eq. 3.6) are a form of likelihood-based regression models.

[3] Average temperature throughout the year shapes the environmental characteristics.

$$E(Y \mid X_1, X_2, ..., X_p) = s_0 + \sum_{j=1}^{p} s_j(X_j) \quad (3.5)$$

$$g(E[Y \mid X_1, X_2, ..., X_p]) = s_0 + \sum_{j=1}^{p} s_j(X_j) \quad (3.6)$$

E stands for expected value; Y is the response variable and $X_1,\ldots X_p$ is the set of predictor variables. $s_i(X)$, $i = 1, \ldots, p$ are smooth functions; g(…) is the link function.

In the additive models, smooth functions replace the regression parameters in a regression model and these functions are standardised so that $\Sigma s_j(X_j) = 0$ (Hastie and Tibshirani, 1986). These functions are estimated by scatter plot smoothers (Hastie and Tibshirani, 1986) of which the most commonly used are splines and locally-weighted regression. The amount of smoothing is controlled by the size of the neighbourhood or bandwidth (Beck and Jackman, 1997). The larger this is, the more smoothing and the more data reduction (eliminating the noise). In locally-weighted regression the amount of smoothing is determined by the span (smaller spans result in tighter neighbourhoods, i.e. using a smaller subset of data points) and in splines the amount of smoothing is determined by the degrees of freedom (d.f.) used (larger d.f. for tighter bandwidths). The form of the response data needs to be specified, as in generalised linear models, through a link function.

GAM were implemented in R (R Development Core Team, 2006) with binomial distribution of error and a logistic link function using the GAM package by Hastie (2006). The smoother used was splines with four degrees of freedom (the number of d.f. and smoother chosen was determined from previous trials and previous studies; Araújo and Luoto, 2007; Meynard and Quinn, 2007; Randin *et al.*, 2006). This package also calculates the AIC values for each model. AUC values were calculated from resubstitution in R using the limma package (Smyth, 2005, 2007).

Analyses

For each model, AIC was determined and the ΔAIC calculated. As suggested by Burnham and Anderson (2002) only the models with ΔAIC of less than 7 were considered. For each model, area under the curve (AUC) of a receiver operating plot (Fielding and Bell, 1997) was calculated through resubstitution. In the text I will refer to this AUC as AUC_{range}. The relationship between AIC and AUC_{range} was examined for each model/species.

For the pseudo-independent data, I randomly split the data in the classic 70% training data – 30% testing data. The average AUC ('Mean AUC') and standard deviation were taken

from 20 fits. The relationship between 'Mean AUC', AUC_{range} and AIC was examined through Spearman correlation and Kruskal-Wallis tests.

Impact on prediction

The models built using all the data were then projected onto the IBA dataset for each of the 12 species and AUC (AUC_{IBA}) was calculated. Spearman correlations were performed for each species with the three AUC values from each evaluation method. This enables the comparison between each measure of model goodness-of-fit and level of prediction accuracy.

Each 70% fit model for all the 10 main models and 10 associated interaction models was used to predict future distribution of the 12 species under climate change. This resulted in 20 possible future predictions to be tested against each future projection built using the full model. The difference between the output from the full-built model and the models built with 70% data was measured using the Mean Absolute Error (MAE, Eq.3.7; Mayer and Butler, 1993). The average MAE and standard deviation were calculated. MAE is more robust than other measures of accuracy such as mean square error (Walther and Moore, 2005).

$$MAE = \left(\sum_i \left| P_i - \Pi_i \right| \right) \Big/ n \qquad (3.7)$$

Where n is the total number of values; P_i is the predicted value i, in this case the models built using 70% of the data, and Π_i is the true value of i, in this case the models built using the full dataset.

The results of this test show how well each model extrapolates (future predictions on to the 30% of the data not used to build the model) compared with the 'truth' (future predictions built with the full data set).

3.1.3 Results

Model selection

AIC varied widely across models for each species, with in most cases only one useful model with $\Delta AIC < 7$. The fit of the models (AUC_{range}) also varied widely from 0.1 to 1 (Tables A1-A8[4]). The maximum AUC for each species ranged from 0.826 to 1 for the breeding ground models and 0.823 to 0.998 for the non-breeding ground models. Data splitting showed that, depending on which random 70% split was used, a very different predictive fit (for the 30%) was achieved, ranging from very poor (0.1) to very good (1). This resulted in some models having high standard deviations about the Mean AUC (Tables A1-A8). On the breeding grounds, the models with an interaction term nearly always showed high standard deviations (Tables A1-A4).

Table 3.3 shows the number of species' distributions each model describes best according to the three model selection techniques. The table shows that AIC and resubstitution favour similar models, while the data splitting technique chooses different and often simpler models, i.e. without an interaction term. Across 220 species, AIC and AUC_{range} were significantly negatively correlated which is what one would expect (Table A9). Indeed 74% of the time the model with the lowest AIC corresponded exactly with the highest AUC_{range}. In the remaining 26%, the lowest AIC corresponded to a model with an AUC difference of between 0-0.02 of that of the highest AUC value. In nine cases (*Anas platyrhynchos, Falco tinnunculus, Tachybaptus ruficollis, Gallinula chloropus, Rallus aquaticus, Tringa totanus, Limicola falcinellus, Scolopax rusticola, and Geronticus eremita*) there was a slight, non-significant positive correlation for the breeding ground values only.

AIC was significantly negatively correlated with Mean AUC for 1% and 43% of species for the breeding and non-breeding models respectively (Table A9), while AUC and Mean AUC were significantly negatively correlated only for 6% and 2% of species for the breeding and non-breeding models respectively (Table A9). Indeed, on the breeding grounds only about 6% of the time did all methods agree, whilst on the non-breeding grounds the percentage was slightly higher (12%).

Interaction models (Mi) were chosen less often by the splitting method. Indeed, there was a difference in the frequency with which the interaction models were chosen depending

[4] Tables and Figures labelled A are in Appendix II.

on which method was used (Kruskal Wallis, d.f. = 2 in all cases: Breeding ground X = 14.932, $p < 0.01$, Winter ground X= 8.286, $p < 0.05$).

There was also a difference in the frequency with which the non interaction models were chosen on the breeding grounds (Kruskal Wallis, X = 9.307, d.f. = 2, $p < 0.05$) but not on the non-breeding grounds (Kruskal Wallis, X = 4.745, d.f. = 2, $p = 0.09$).

Table 3.3: Models (refer to Table 3.2) and associated number of species for which each model is the "best" as measured by three different model selection techniques (lowest AIC, highest AUC or highest Mean AUC from the data splitting technique).

models	breeding			Non-breeding		
	AIC	AUC_{range}	split	AIC	AUC_{range}	split
M1	1	0	5	4	0	11
M2	0	0	2	3	0	5
M3	1	0	40	3	0	47
M4	1	0	17	2	0	22
M5	37	39	8	1	2	0
M6	14	16	6	0	0	3
M7	16	2	14	2	0	46
M8	3	1	7	6	5	48
M9	6	0	99	9	7	0
M10	1	0	29	4	4	0
M1i	0	0	0	1	0	11
M2i	1	1	0	1	0	9
M3i	3	2	0	20	25	5
M4i	7	3	1	14	14	13
M5i	4	7	0	6	7	0
M6i	7	11	0	10	16	0
M7i	27	39	0	27	22	0
M8i	28	31	0	39	43	9
M9i	40	46	1	30	34	0
M10i	32	31	0	47	50	0

Robustness and generality

This section deals with the results using the sub-set of 12 species (Table 3.1). The fit of the models (AUC_{range}) ranged from species to species (Table 3.4). The performance of the simple models (using either prevalence or one or two variables) ranged from AUC_{range} 0.495 (a performance no different from random) to 0.994 (excellent). However, for each species an excellent fit could be found through one of the simple models including a climatic variable (See Appendix IIIa). The main models' AUC_{range} ranged from 0.624 to 0.997, whilst the interaction models' performance ranged from 0.403 to 0.997 (Table 3.4).

For each species it is possible to select the best model according to the different model selection techniques. Table 3.5 shows the results of 20 fits (main models only with their associated interaction models) and highlights the model chosen by the other methods. Seven out of all the possible models recur as the best models according to resubstitution (Table 3.4 and 3.5); these are the four variable models with, nine times out of twelve, a model including PPE either before or during the breeding season. Also for nine of the species the best model, i.e. highest AUC_{range}, includes an interaction. AIC selected the same model as AUC_{range} apart from in two cases. For all but three species only one model was selected by AIC as the ΔAIC for the other models were much larger than 7.

The 20 70-30 split results (Table 3.5) showed that it is possible to obtain a wide variety of AUC depending on the randomly chosen split. The standard deviations show, especially for the interaction models, that depending on which split is made, one may get a false sense of how well the model performs. With the 20 70-30 splits one can identify the most robust model, i.e. high mean AUC and low standard deviation. The most robust model is always different from that chosen as 'best model' from AIC and resubstitution. Moreover, all the interaction models are not robust. This disparity between AUC_{range} and Mean AUC indicates over-fitting. The effect of over-fitting on future predictions is shown in Figure 3.2. Figure 3.2 shows for each species the average MAE of each model. All models with an interaction term have wide error bars and large MAE. Most of the main models are robust in their future projections though models 5 and 6 (including average PPE) are not robust for many species.

Table 3.4: AUC values for the full models and AUC for IBA data predicted from the full models. Refer to Table 3.2 for model description.

Full models	*A. nisus*	*G. fulvus*	*P. apivorus*	*C. ruficollis*	*C. morinellus*	*H. rustica*	*L. nubicus*	*P.porzana*	*A. hypoleucos*	*L. lapponica*	*S. communis*	*S. undata*
m1	0.945	0.838	0.955	0.888	0.975	0.919	0.892	0.947	0.935	0.996	0.980	0.980
m1i	0.953	0.859	0.962	0.892	0.977	0.926	0.911	0.951	0.944	0.997	0.983	0.981
m2	0.941	0.843	0.952	0.882	0.970	0.913	0.888	0.946	0.932	0.997	0.979	0.982
m2i	0.951	0.858	0.960	0.885	0.973	0.922	0.904	0.565	0.240	0.510	0.982	0.985
m3	0.948	0.846	0.955	0.895	0.976	0.932	0.900	0.954	0.936	0.996	0.982	0.983
m3i	0.955	0.865	0.963	0.898	0.978	0.937	0.916	0.957	0.946	0.997	0.984	0.984
m4	0.943	0.849	0.952	0.884	0.971	0.924	0.899	0.952	0.933	0.997	0.981	0.984
m4i	0.953	0.860	0.961	0.889	0.974	0.932	0.915	0.563	0.545	0.508	0.983	0.987
m5	0.978	0.838	0.903	0.932	0.980	0.982	0.960	0.800	0.957	0.834	0.960	0.965
m5i	0.948	0.840	0.870	0.754	0.868	0.952	0.572	0.797	0.768	0.838	0.915	0.912
m6	0.977	0.826	0.890	0.626	0.976	0.982	0.962	0.951	0.957	0.751	0.927	0.935
m6i	0.947	0.775	0.894	0.939	0.977	0.961	0.572	0.901	0.835	0.776	0.906	0.964
m7	0.975	0.920	0.967	0.624	0.982	0.978	0.737	0.955	0.951	0.882	0.985	0.748
m7i	0.979	0.928	0.969	0.969	0.984	0.981	0.403	0.955	0.958	0.806	0.986	0.887
m8	0.974	0.922	0.965	0.970	0.978	0.978	0.956	0.631	0.948	0.999	0.984	0.920
m8i	0.978	0.927	0.968	0.633	0.980	0.981	0.635	0.878	0.958	0.999	0.985	0.930
m9	0.975	0.919	0.963	0.978	0.978	0.976	0.942	0.955	0.955	0.997	0.984	0.984
m9i	0.978	0.926	0.967	0.980	0.980	0.979	0.946	0.956	0.962	0.997	0.986	0.984
m10	0.972	0.917	0.959	0.980	0.975	0.975	0.943	0.954	0.952	0.998	0.983	0.985
m10i	0.978	0.924	0.964	0.980	0.979	0.979	0.947	0.956	0.962	0.998	0.985	0.987

Table 3.4 continued

IBAmodels	*A. nisus*	*G. fulvus*	*P. apivorus*	*C. ruficollis*	*C. morinellus*	*H. rustica*	*L. nubicus*	*P.porzana*	*A. hypoleucos*	*L. lapponica*	*S. communis*	*S. undata*
m1	0.611	0.741	0.735	0.923	0.896	0.653	0.887	0.829	0.716	0.987	0.735	0.941
m1i	0.652	0.585	0.774	0.482	0.911	0.753	0.775	0.838	0.694	0.869	0.731	0.477
m2	0.597	0.734	0.736	0.934	0.897	0.622	0.906	0.813	0.717	0.780	0.722	0.943
m2i	0.683	0.555	0.738	0.934	0.909	0.747	0.776	0.815	0.645	0.653	0.699	0.476
m3	0.611	0.761	0.737	0.921	0.898	0.652	0.913	0.828	0.715	0.985	0.735	0.941
m3i	0.631	0.553	0.600	0.835	0.752	0.734	0.775	0.844	0.733	0.642	0.741	0.865
m4	0.595	0.757	0.740	0.930	0.897	0.621	0.918	0.808	0.717	0.985	0.723	0.943
m4i	0.615	0.580	0.714	0.835	0.902	0.645	0.780	0.720	0.733	0.649	0.756	0.947
m5	0.601	0.679	0.756	0.808	0.904	0.638	0.894	0.633	0.736	0.676	0.691	0.887
m5i	0.688	0.656	0.740	0.812	0.717	0.759	0.774	0.827	0.715	0.670	0.740	0.882
m6	0.594	0.691	0.720	0.482	0.899	0.618	0.907	0.804	0.738	0.647	0.702	0.747
m6i	0.673	0.578	0.663	0.870	0.911	0.754	0.776	0.822	0.710	0.710	0.732	0.870
m7	0.616	0.641	0.730	0.767	0.906	0.641	0.914	0.815	0.723	0.806	0.728	0.874
m7i	0.689	0.673	0.654	0.743	0.684	0.707	0.776	0.644	0.671	0.876	0.710	0.480
m8	0.608	0.579	0.737	0.937	0.908	0.621	0.774	0.666	0.727	0.854	0.729	0.945
m8i	0.668	0.760	0.753	0.504	0.918	0.700	0.832	0.640	0.759	0.807	0.724	0.474
m9	0.611	0.767	0.729	0.933	0.891	0.653	0.905	0.831	0.724	0.987	0.735	0.940
m9i	0.568	0.659	0.712	0.506	0.867	0.753	0.775	0.716	0.742	0.653	0.718	0.856
m10	0.597	0.754	0.730	0.939	0.892	0.615	0.916	0.824	0.718	0.645	0.670	0.945
m10i	0.674	0.589	0.763	0.809	0.909	0.742	0.832	0.825	0.738	0.653	0.739	0.853

Table 3.5: Average AUC and standard deviation for the 20 70-30 splits for each main model for 12 species (^{W} indicates the widespread species). The * denotes the most robust model. The $^{+}$ denotes the model chosen as best by resubstitution. The $^{\#}$ denotes the model chosen by AIC selection. And ± denotes model chosen by both AIC and AUC. Refer to Table 3.2 for description of models.

	m1		m2		m3		m4		m5		m6		m7		m8		m9		m10	
Models	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ
Accipiter nisus^{w}	0.973	0.003	0.972	0.003	0.974	0.003	0.973	0.003	0.946	0.053$^{\#}$	0.938	0.049	0.974	0.003	0.973	0.003	**0.975**	**0.003***	0.974	0.003
Gyps fulvus	0.905	0.012	0.902	0.012	0.912	0.011	0.911	0.011	0.694	0.161	0.697	0.134	0.644	0.145	0.680	0.163	**0.914**	**0.011***	0.910	0.011
Pernis apivorus^{w}	**0.954**	**0.004***	0.951	0.005	0.954	0.004	0.952	0.005	0.843	0.098	0.828	0.106	0.897	0.117	0.924	0.057	0.955	0.004	0.953	0.004
Caprimulgus ruficollis	0.965	0.004	0.973	0.002	0.973	0.003	0.977	0.003	0.679	0.213	0.717	0.203	0.760	0.198	0.850	0.200	0.975	0.003	**0.978**	**0.002***
Charadrius morinellus	0.972	0.008	0.968	0.008	0.940	0.143	0.957	0.055	0.967	0.011	0.963	0.010	0.973	0.008	0.969	0.008	**0.973**	**0.007***	0.970	0.007
Hirundo rustica^{w}	0.980	0.003	0.980	0.003	0.980	0.003	0.980	0.003	0.980	0.003±	0.980	0.003±	0.980	0.002	**0.980**	**0.002***	0.980	0.003	0.980	0.003
Lanius nubicus	0.953	0.008	0.957	0.009	**0.966**	**0.008***	0.964	0.008	0.720	0.224±	0.686	0.223±	0.888	0.186	0.586	0.129	0.960	0.008	0.962	0.009
Porzana porzana^{w}	0.947	0.006	0.946	0.007	**0.953**	**0.006***	0.952	0.006	0.788	0.168	0.761	0.190	0.918	0.090	0.785	0.179	0.949	0.006	0.949	0.006
Actitis hypoleucos^{w}	0.950	0.005	0.951	0.005	0.951	0.005	0.951	0.005	0.949	0.020	0.949	0.022	0.952	0.005	0.951	0.005	**0.954**	**0.004***	0.954	0.005
Limosa lapponica	0.996	0.001	0.896	0.185	0.996	0.002	0.991	0.024	0.799	0.160	0.796	0.173	0.828	0.134	0.827	0.148^{+}	**0.997**	**0.001***	0.914	0.181
Sylvia communis^{w}	0.945	0.033	0.880	0.062	**0.964**	**0.004***	0.963	0.004	0.891	0.054	0.861	0.021	0.843	0.130	0.926	0.049	0.959	0.004	0.892	0.050
Sylvia undata	0.977	0.003	0.976	0.003	**0.978**	**0.003***	0.977	0.003	0.732	0.211	0.666	0.209	0.757	0.223	0.817	0.210	0.977	0.003	0.977	0.003
With Interaction																				
Accipiter nisus^{w}	0.877	0.114	0.890	0.035	0.898	0.030	0.874	0.130	0.884	0.042	0.892	0.027	0.893	0.028^{+}	0.888	0.029	0.893	0.049	0.901	0.042
Gyps fulvus	0.714	0.104	0.681	0.155	0.746	0.135	0.740	0.116	0.691	0.110	0.668	0.120	0.746	0.123±	0.687	0.123	0.683	0.147	0.672	0.120
Pernis apivorus^{w}	0.827	0.085	0.802	0.157	0.835	0.088	0.847	0.123	0.832	0.058	0.834	0.070	0.827	0.069±	0.827	0.079	0.826	0.077	0.833	0.109
Caprimulgus ruficollis	0.664	0.163	0.768	0.210	0.736	0.205	0.723	0.215	0.697	0.208	0.704	0.218	0.668	0.204	0.725	0.220	0.682	0.212±	0.822	0.195±
Charadrius morinellus	0.741	0.187	0.906	0.142	0.768	0.160	0.764	0.178	0.727	0.106	0.940	0.078	0.735	0.096	0.900	0.116	0.662	0.152	0.818	0.195
Hirundo rustica^{w}	0.929	0.031	0.953	0.034	0.882	0.115	0.962	0.033	0.934	0.028	0.937	0.032	0.921	0.028	0.932	0.094	0.923	0.030	0.941	0.044
Lanius nubicus	0.602	0.180	0.635	0.210	0.586	0.139	0.584	0.125	0.510	0.064	0.607	0.136	0.559	0.123	0.634	0.181	0.554	0.154	0.652	0.186
Porzana porzana^{w}	0.795	0.150	0.949	0.006	0.735	0.144±	0.796	0.165	0.778	0.100	0.775	0.110	0.761	0.093	0.763	0.119	0.787	0.142	0.942	0.044
Actitis hypoleucos^{w}	0.844	0.084	0.855	0.066	0.831	0.096	0.907	0.079	0.871	0.076	0.847	0.074	0.820	0.047	0.816	0.061	0.860	0.120	0.832$^{\#}$	0.068^{+}
Limosa lapponica	0.647	0.204	0.816	0.212	0.627	0.163	0.685	0.238	0.799	0.116	0.801	0.135	0.784	0.117	0.738	0.143	0.669	0.198$^{\#}$	0.758	0.223
Sylvia communis^{w}	0.832	0.072	0.881	0.046	0.866	0.023	0.906	0.103	0.857	0.032	0.861	0.021	0.839	0.051±	0.868	0.032	0.864	0.040	0.865	0.041
Sylvia undata	0.605	0.182	0.673	0.218	0.743	0.206	0.817	0.200	0.685	0.211	0.744	0.187	0.722	0.207	0.588	0.171	0.636	0.189	0.733	0.216±

The independent validation (Table 3.4) shows that in most cases my models are not transferable. All models for *Accipiter nisus* perform very badly (AUC 0.597-0.688). For the other species at least one model gives AUC_{IBA} values above 0.7, the threshold for a useful model, and for five species some models are excellent (AUC_{IBA} above 0.9). The 'best model' according to the highest AUC_{IBA} is different to the models chosen by model selection methods. However, the highest AUC may not always be the best selector as there is no rule to say when an AUC value is different from another one like the delta AIC for example.

To investigate the relationship between the different AUCs, I correlated all the AUC values (AUC_{range}, AUC_{IBA} and Mean AUC). The results of the Spearman correlations are in Table 3.6. Visual appraisals of two of the relationships between AUCs are shown in Figures 3.3 and 3.4. These figures distinguish between the different models (simple, main and interactions). The correlations showed that for most species the full fitted AUC_{range} and Mean AUC are correlated with $AUC_{IBA.}$ For most cases these were (as one would expect) strong positive correlations. However, for *Accipiter nisus* and *Hirundo rustica* the correlations were negative. Although both AUC_{range} and Mean AUC provided similar correlations coefficients, Mean AUC often had a stronger correlation with AUC_{IBA}. Moreover, when comparing Fig. 3.3 and 3.4, it can be seen that AUC_{range} often gives a false impression of the performance of interaction models (Fig 3.3 b ,d ,h ,j and l) whereas the Mean AUC does not (Fig 3.4 b, d, h, j and l) in terms of how well the interaction models extrapolate.

Table 3.6: Spearman correlation between Resubstitution AUC (R), Mean AUC (M) and IBA AUC (I). * indicate level of significance

Species	R-M rho	R-I rho	M-I rho
Accipiter nisus	0.301	-0.162	-0.538**
Gyps fulvus	0.101	0.200	0.775***
Pernis apivorus	0.134	0.184	0.237
Caprimulgus rufficolis	0.327*	0.432**	0.825***
Charadrius morinellus	0.183	0.595***	0.359*
Hirundo rustica	0.045	-0.320	-0.547***
Lanius nubicus	0.299	0.349*	0.729***
Porzana porzana	0.367*	0.503**	0.514**
Actis hypoleucos	0.116	0.394*	0.091
Limosa lapponica	0.258	0.355*	0.711***
Sylvia communis	0.207	0.367*	-0.087
Sylvia undata	0.234	0.438**	0.698***

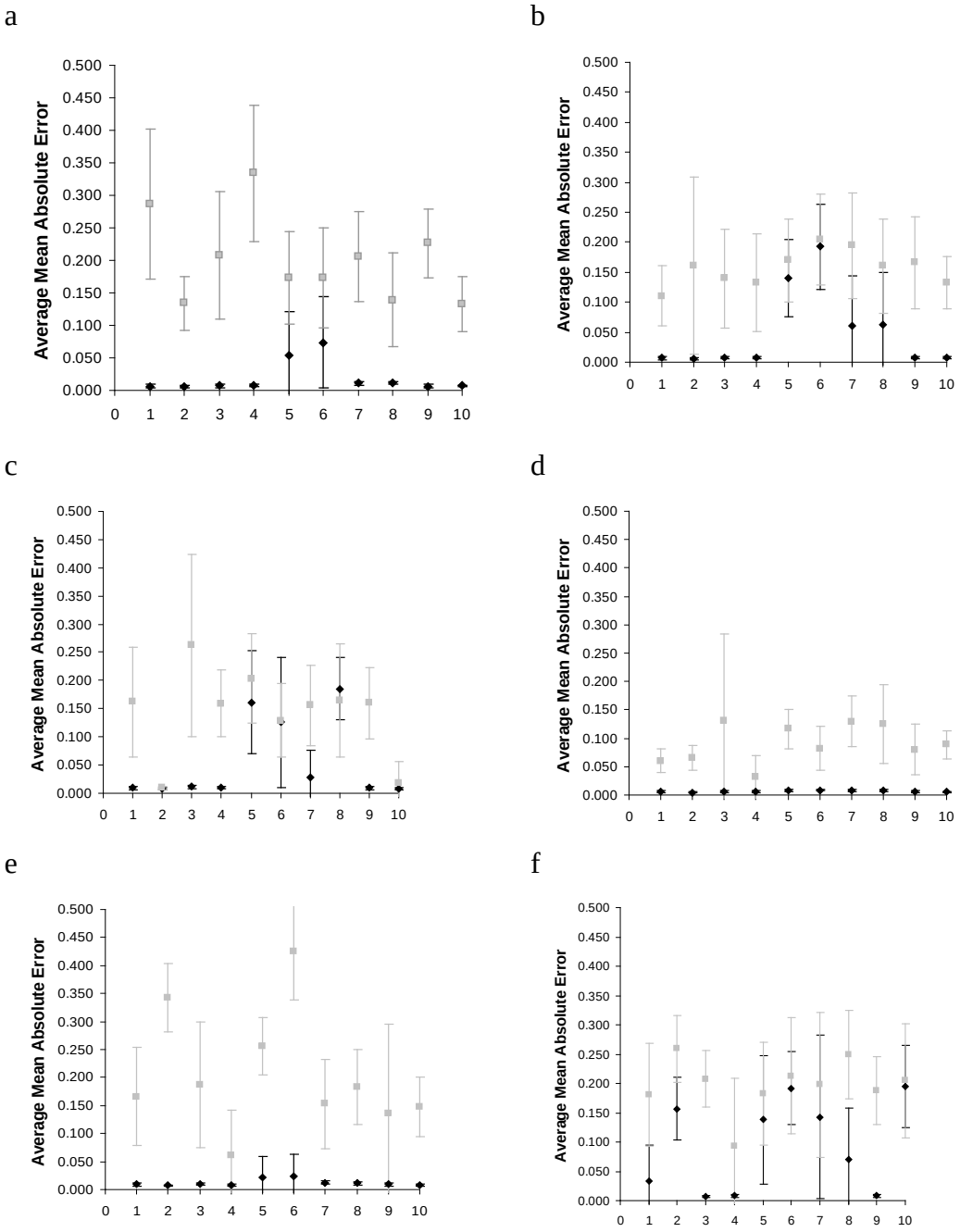


Figure 3.2: Mean absolute error in future scenario probabilities for models 1-10 with (light grey squares) and without interactions (black diamonds) for widespread species a) *Accipiter nisus*, b) *Pernis apivorus*, c) *Porzana porzana*, d) *Hirundo rustica*, e) *Actis hypoleucos*, f) *Sylvia communis*

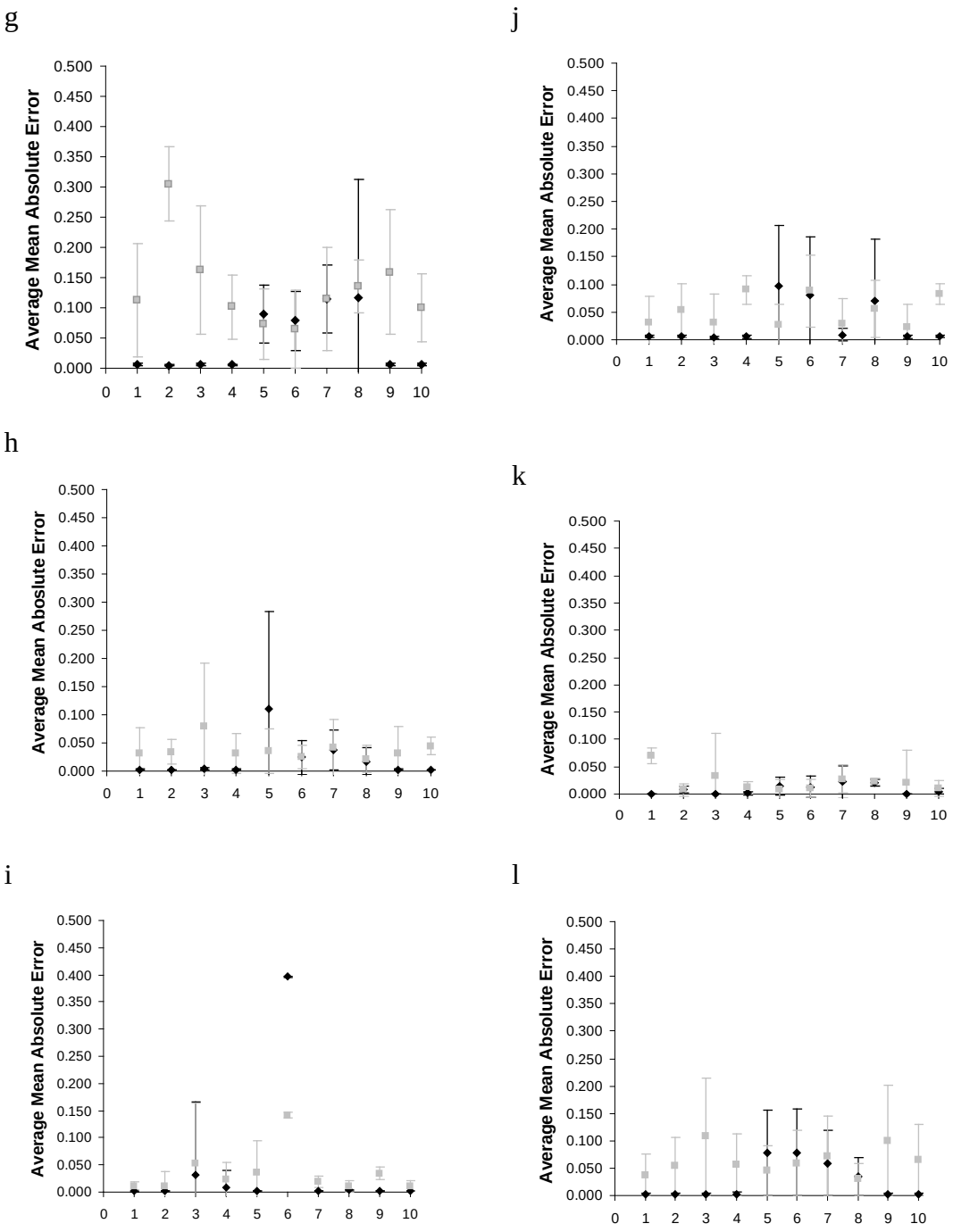


Figure 3.2: Mean absolute error in future scenario probabilities for models 1-10 with (light grey squares) and without interactions (black diamonds) for restricted species g) *Gyps fulvus*, h) *Caprimulgus rufficolis*, i) *Charadrius morinellus*, j) *Lanius nubicus*, k) *Limosa lapponica* l) *Sylvia undata*

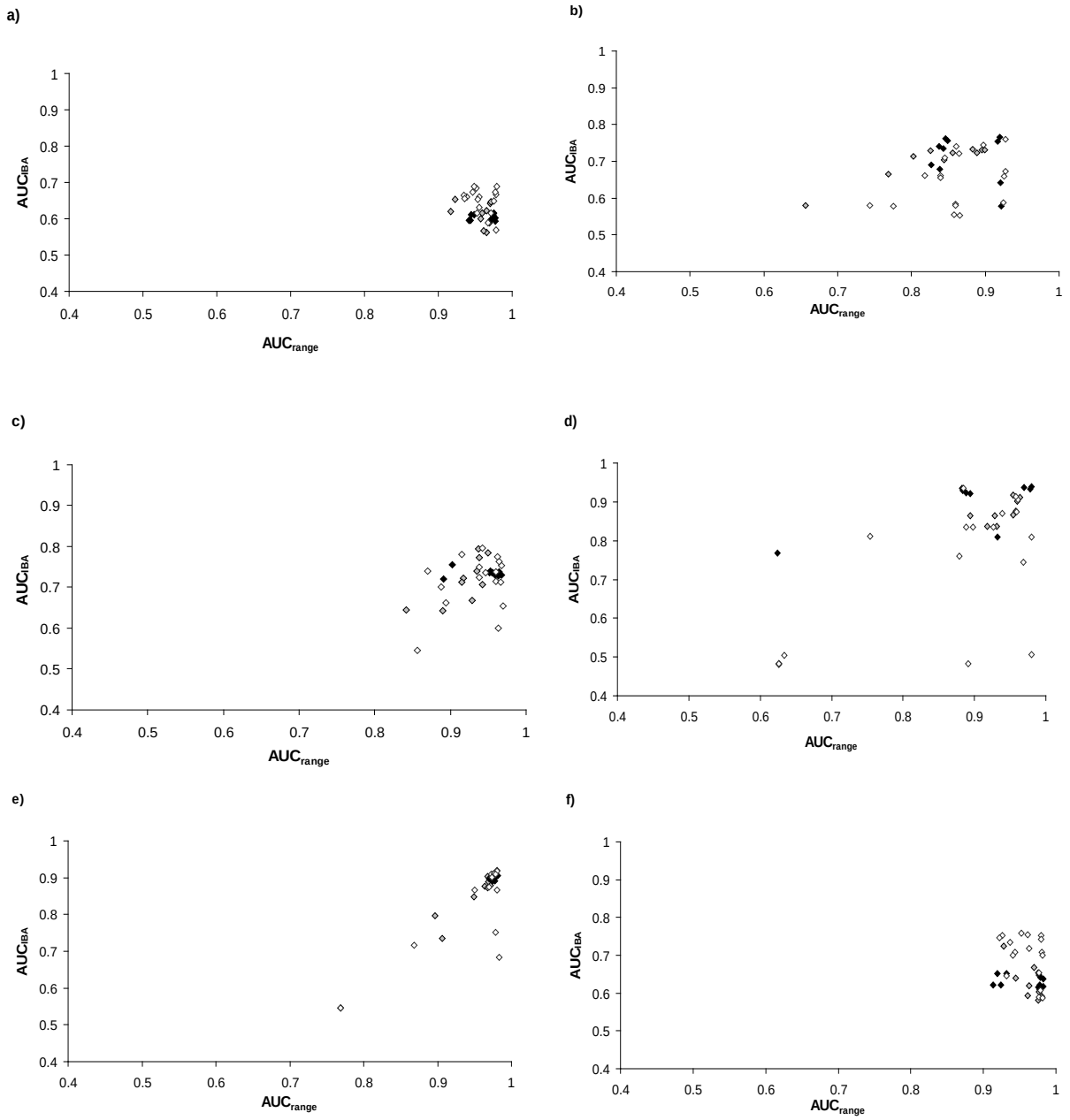


Figure 3.3: Relationship between AUC_{IBA} and AUC_{range} for species: a) *Accipiter nisus*, b) *Gyps fulvus*, c) *Pernis apivorus*, d) *Caprimulgus ruficollis*, e) *Charadrius morinellus*, f) *Hirundo rustica*. Grey dots represent simple models, black dots represent main models and white dots represent interaction models.

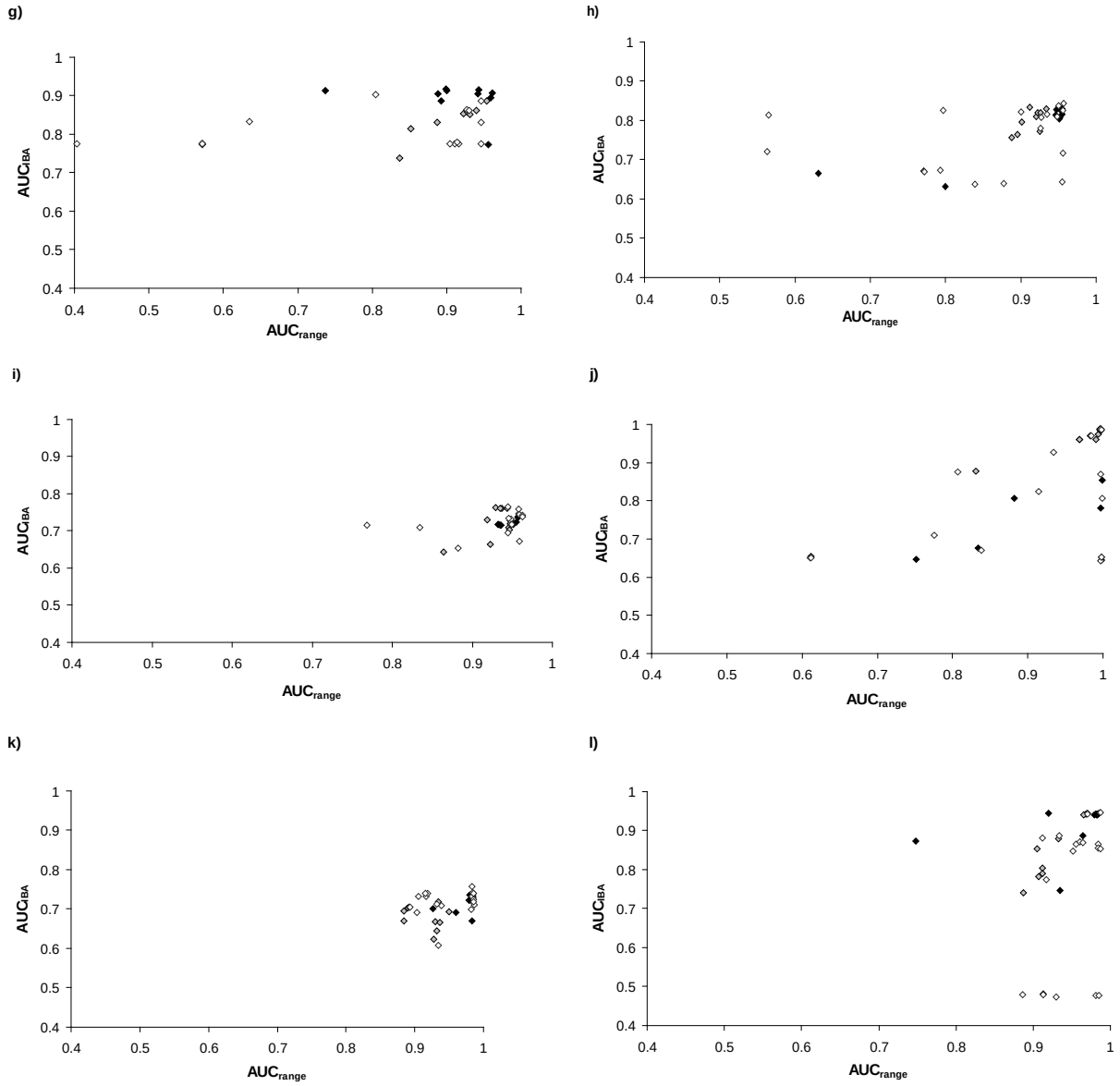


Figure 3.3: Relationship between AUC_{IBA} and AUC_{range} for species: g) *Lanius nubicus*, h) *Porzana porzana*, i) *Actis hypoleucos*, j) *Limosa lapponica*, k) *Sylvia communis*, l) *Sylvia undata*. Grey dots represent simple models, black dots represent main models and white dots represent interaction models

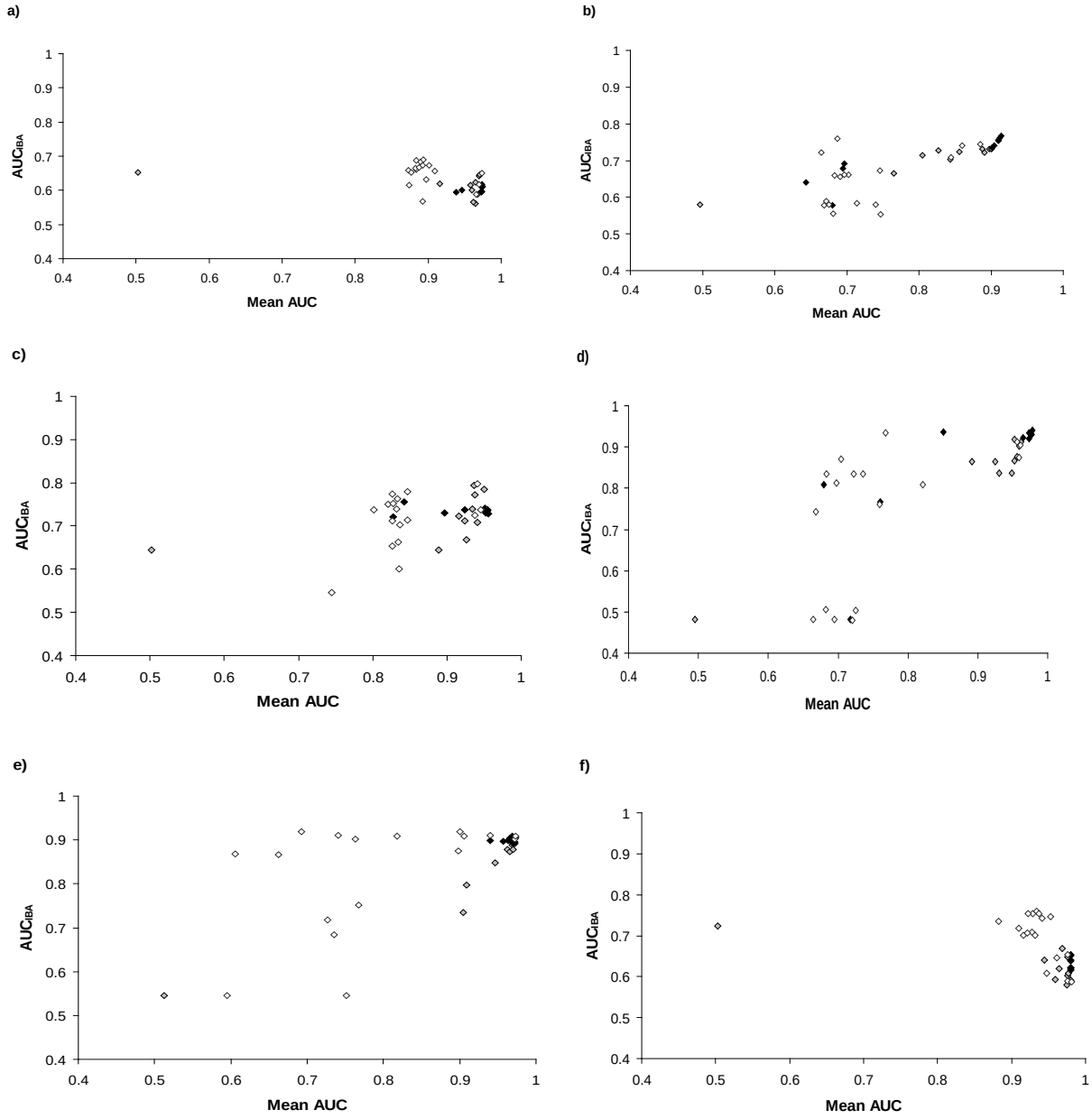


Figure 3.4: Relationship between AUC_{IBA} and Mean AUC for species: a) *Accipiter nisus*, b) *Gyps fulvus*, c) *Pernis apivorus*, d) *Caprimulgus ruficollis*, e) *Charadrius morinellus*, f) *Hirundo rustica*. Grey dots represent simple models, black dots represent main models and white dots represent interaction models.

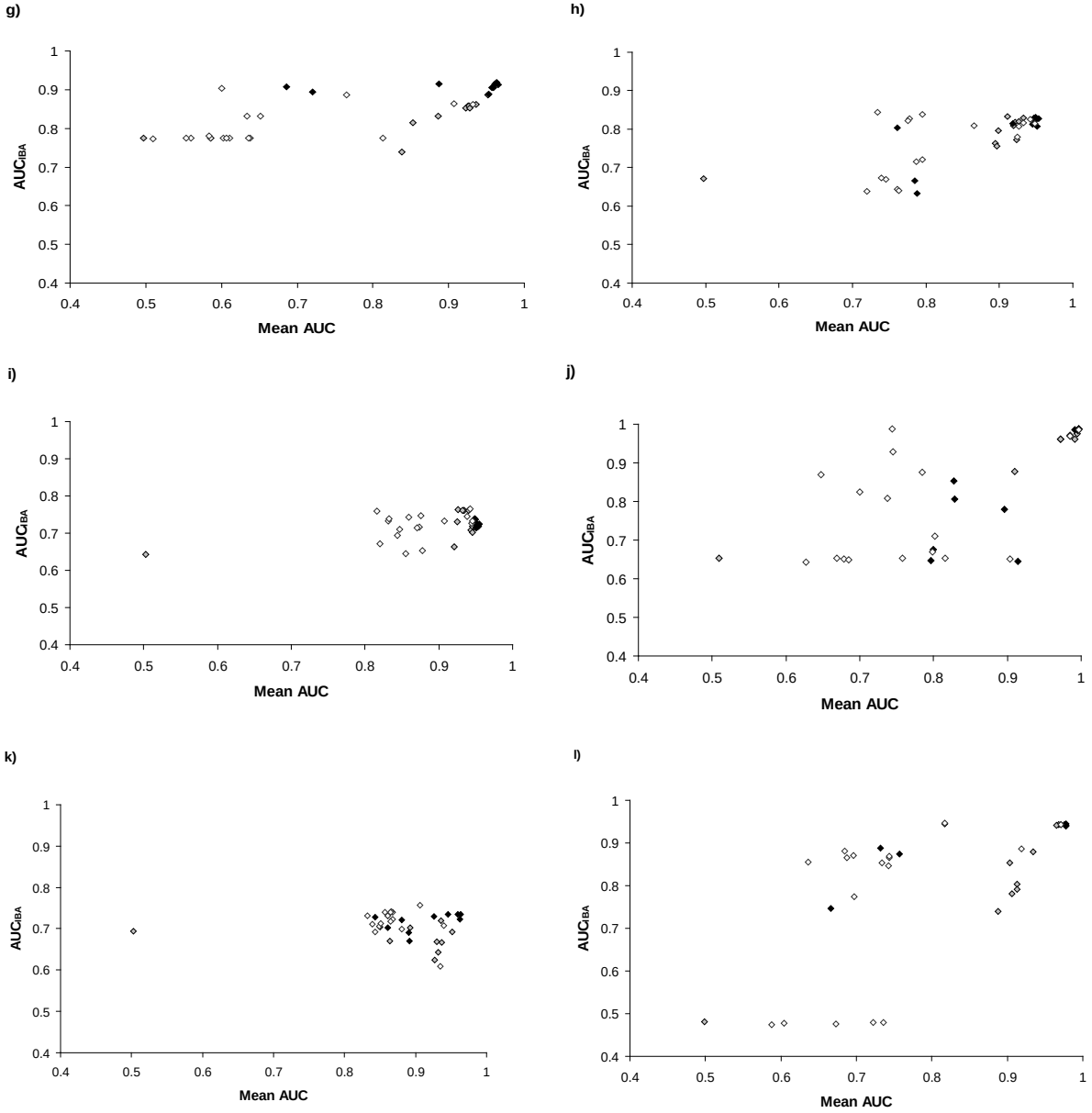


Figure 3.4: Relationship between AUC_{IBA} and Mean AUC for species: g) *Lanius nubicus*, h) *Porzana porzana*, i) *Actis hypoleucos*, j) *Limosa lapponica*, k) *Sylvia communis*, l) *Sylvia undata*. Grey dots represent simple models, black dots represent main models and white dots represent interaction models.

3.1.4 Discussion

In this study, I built 20 models (10 of which included interaction terms) representing the potential description of the species-environment relationships. In addition, for 12 species, reduced models were built (see Appendix IIIa). The results show that each species can be modelled well (AUC_{range} above 0.8) as long as the appropriate combination of variables for each species is used. Finding such good model fits in our sample of 12 species with only one or two variables is very surprising and counter to the many-variable models found in the literature (Bakkenes *et al.*, 2002; Buckland and Elston, 1993; Corsi *et al.*, 1999). However, as these simple variables were chosen to be biologically and ecologically meaningful, this finding demonstrates the conceptual validity of our base models (Rykiel, 1996). A recent study by Beale *et al.* (2008) suggested that species may not be entirely constrained by climate. They modelled the distribution of bird species using bioclimatic variables and using a null model. They found that their null model produced valid simulations of species' distribution and a subsequent power analysis did not reveal that species' distributions patterns were determined by climate. Although some of my null models produced adequate model fits (see Appendix IIIa), models including climatic variables performed much better. Beale *et al.* (2008) suggest that maybe other factors, such as biotic interactions, are more important in shaping species' distributions, although they concede that, for some species, climate was important in determining their distribution. It may be that the data available may not have enough distinguishing power for the addition of even known important factors.

Many different models performed well in terms goodness-of fit, making it difficult to choose among them. The information-theoretic approach (AIC) enables one to choose a specific model for each species, especially since in this study, only one model had a good delta AIC. AUC and AIC were found to select similar models. However, the data splitting method, which aims to reveal the most robust predictive model, highlighted different models to those selected by either AIC or AUC. These analyses also showed that more complex models, although they perform better (in terms of internal validity found through resubstitution), actually over-fit the data (Fielding, 2002). Over-fitting is a problem especially when the purpose of a model is to predict or extrapolate (Araújo and Guisan, 2006). Variable selection is often used as a regularisation method, i.e. as means of balancing model fit and complexity. Reineking and Schröder (2006) examined the effects of variable selection through AIC on model predictive performance as compared with other regularization methods (least absolute shrinkage and selection operator (*lasso*), and penalised maximum likelihood (*ridge*)) and found that although AIC was the best among variable selection procedures, it was

not as good as *ridge*. However, no studies have looked at variable selection methods and a model's predictive power.

It is not only the complexity of the inputted variables that can cause over-fitting but also the method chosen for the model which engenders this problem, as Randin *et al.* (2006) highlight. Indeed, GAM have a great flexibility to 'curve-fit', which can be problematic if it results in overfitting. However, many studies show GAMs' excellence in species' distribution modelling (Araújo *et al.*, 2005; Elith *et al.*, 2006). It is therefore vital to ensure that any model intended for prediction does not over-fit the data and that it is robust. My results show that resubstitution and model selection via AIC give no indication of a model's robustness. The fact that AIC and AUC chose similar models is good, however, if one is looking to use the models for descriptive or explanatory purposes (Araújo and Guisan, 2006). In this case, AIC may be more useful than AUC as it is penalises for the number of parameters used. Moreover, GAM have, instead of a parameter for each variable, a smooth function which can increase the number of parameters. This fact explains why in some cases AIC and AUC differ. However, my results also show that AIC sometimes selects more complex models than AUC. This result was also found by Maggini *et al.* (2006). More research is be needed into AIC and prediction.

All modellers agree that to validate properly a predictive species distribution model, an independent data set is required. This is not always available and so a pseudo independent data set is created by splitting the data in some way, either through a single split or cross-validation. However, splitting the data once randomly (as done by many studies, see Chapter 2) does not show model robustness, generality or transferability. In this study I took 20 random 70-30 splits. The results showed (standard deviations in Table 3.5 and Tables A1-A8) that this can change the predictive performance of the models. Robustness is an important quality for models especially if these models are to extrapolate to different areas or time periods. The effect of non-robust models on extrapolations into a future time period is shown in Fig. 3.2. The interaction models show higher Mean Absolute Error in future predictions along with higher standard deviations than the non-interaction models. This was also the case for some non-interaction models. This shows that different predictions are generated depending on how much data are available, which is a sign that the overall models over-fit. Projecting the potential effect of climate change on species' range is already fraught with uncertainty (Araújo *et al.*, 2005; Pearson *et al.*, 2006; Thuiller, 2004) without introducing more uncertainty with a non-robust model. Moreover, more often than not the high goodness-of-fit of these complex models do not translate to good fits when projecting onto a new data set (Fig 3.3 and 3.4). This reinforces the fact that more complex models do not transfer as

well. Nevertheless, the right interaction in the right model can provide a better model (Table 3.4). However, without independent tests, interactions vastly over-fit the data and decrease a model's generality (Vaughan and Ormerod, 2005).

Validation with an independent data set revealed two things. First, that many of my models do not transfer well as Randin *et al.* (2006) and McAlpine *et al.* (2008) also found; and second that the traditional methods for validating a model without an independent data set (resubstitution and a one time split; Fielding & Bell, 1997) do not give the 'best model' (highest AUC_{IBA}) in terms of transferability. Even the most robust model from the 20 70-30 splits did not pick out the 'best model'. This is problematic especially as there are no guidelines to goodness-of-fit measures such as with the information-theoretic approach. However, my results show that mean AUC is a better determinant of a good predictive model than other methods (Fig. 3.3 and 3.4). This result agrees with Maggini *et al.'s* (2006) experiments using GAM. They tested five methods for model selection and found that model selection based on cross-validation provided a model that was more stable and parsimonious than other methods. My study further shows that this method corroborates with independent validation (Table 3.6).

For the majority of species, a positive correlation between mean AUC and AUC_{IBA} was found. Two species (*Accipiter nisus* and *Hirundo rustica*), however, had strong negative correlations between mean AUC and AUC_{IBA}. The quality of the independent data set or other factors may account for this discrepancy. For instance, the time and effort given to collect both our original data set and the validation data set may not match. Alternatively, areas may be modelled as suitable for the species in which it is actually not found solely due to persecution or destruction of habitat. *Accipiter nisus* is a persecuted raptor and therefore the independent data set may contain many false negatives. *Hirundo rustica*, on the other hand, is a widespread species in Europe. Many widespread species are under-recorded in datasets such as IBAs as these were set up to protect rarer species and so common species are not recorded. These discrepancies highlight the fact that having an appropriate independent data set is important. This validation may, therefore, not be useful as a basis for validating all migratory bird models, though provides some interesting points on the quality of independent data sets.

The transferability study although is based only on twelve species, tried to select a mix of widespread and range restricted species. The final selection of species may not necessarily been the best as highlighted in the discussion above. Furthermore, although the total number of species was appropriate for the analyses, the number of widespread and range restricted species may have been too few to make any proper assertions. Future study could be done to

get more robust results[5]. However, my results revealed some differences between widespread and less prevalent species. Indeed the correlations between AUC and AUC_{IBA} were stronger for less prevalent species and their future predictions were more robust, indicating better models. Whether this is a question of ecology or purely due to prevalence is not known. AUC is not generally thought to be affected by prevalence (Manel *et al.*, 2001; McPherson, Jetz and Rogers, 2004). However, Maggini *et al.* (2006) found that AUC was affected by very high prevalence (above 0.8).

3.1.5 Conclusion

The ecology of species is important when modelling species' distributions and the choice of variables in the models will affect model fit (Araújo and Guisan, 2006). Although the base combination of variables (Huntley *et al.*, 2006; Huntley *et al.*, 2004) chosen modelled species' distributions well (m1 and m2), adding finely tuned variables, i.e. variables measured for the time period when the migratory bird is on its breeding grounds (m7-m10), created a better model (Heikkinen *et al.* 2006 also found this).

The main finding of this section is that goodness-of-fit based on resubstitution provided an overoptimistic result and also hid the potential over-fitting of the models. Araújo *et al.* (2005) found that data partitioning provided over-optimistic results in terms of how well a model performs on an independent data set. However, my results also highlight the problems of taking only one 70-30 split. A more accurate idea of the model's robustness is achieved by selecting multiple fits. However, in light of certain criticisms of AUC, and of the dearth of studies that compare model selection and model validation techniques, more research is needed in this field.

[5] Working on more species for this study was outside the scope of the thesis, as the main point was determining the potential impacts of climate change on species (Chapter 4 & 5).

3.2 Species distribution models: method selection

3.2.1 Introduction

Choosing an appropriate method to model species' distribution is difficult in view of the vast array of methods now available to the scientific community (Elith and Burgman, 2003; Elith *et al.*, 2006; Guisan and Zimmermann, 2000). The choice of method is mainly dependent on the type of data (see Chapter 2) and the purpose of the model (mechanistic, descriptive or predictive). The data available for this study are presence-absence data, so a choice of statistical methods can be used. There is a large evidence base supporting log-likelihood regression methods, like generalised linear models (GLM) and generalised additive models (GAM), for species distribution models (SDM). These methods have the ability to model realistically the species-environment relationships (Austin, 2002) and have been used extensively (Balbontin, 2005; Brotons *et al.*, 2004; Randin *et al.*, 2006; Thuiller, 2003). GAM were discussed in the previous section and are semi-parametric extensions of GLM. GLM (Eq. 3.9) are generalisations of the linear model (Eq.3.8)

$$Y = b_0 + b_1 X_1 + b_2 X_2 + ... + b_k X_k \quad (3.8)$$

$$g\left(E\left[Y \mid X_1, X_2, ..., X_k\right]\right) = b_1 X_1 + b_2 X_2 + ... + b_k X_k \quad (3.9)$$

Where E stands for expected value; Y is the response variable and $X_1,\ldots X_k$ is the set of predictor variables; b_0 is the regression coefficient for the intercept and the b_i values are the regression coefficients (for variables 1 through k) computed from the data. The generalised form includes a link function for the expected value of Y: g(...). This allows distribution of the response variable to be non-normal and not continuous if necessary.

GLM are less flexible than GAM because the values are predicted from a linear combination of predictor variables. However, they are still popular because of their statistical grounding and the ease of interpretation of results compared to GAM. Moreover, in a recent study by Radin *et al.* (2006), GLM produced distribution models that were more transferable than GAM.

Despite the popularity of these regression methods, many other methods have appeared in recent years (see Elith *et al.*, 2006) that are supposed to surpass the old ones. However, it is important to consider the capabilities of the model in conjunction with the objectives. For instance, the maximum entropy methods (Phillips, Anderson and Schapire,

2006) are designed for sparse presence-only data, and boosted regression trees (Friedman, Hastie and Tibshirani, 2000) have a tendency to over-fit (StatSoft Inc., 2007), which is not a good trait for a predictive model.

With presence-absence data there is a strong case to use regression-based methods. Another method that has had some success is based on climate envelopes: Climate Response Surfaces (CRS; Huntley *et al.*, 1995) or Smoothed Response Surfaces (SRS; Gavin and Hu, 2005). These techniques develop response surfaces based on the relative frequency of points (species' presences or absences) in climate space. The relationship between the predictor variables and the response variable is fitted through locally-weighted regression (LOESS). In LOESS simple models are fitted to localized subsets of the data to build a smooth function. Using LOESS has the benefit of making no assumption about the form of the species-environment relationship (Huntley *et al.*, 2007). GAM have a similar advantage in that often splines or LOESS are used. In CRS's use of LOESS, however, the model is fitted as a single function of all predictors which is in contrast to GAM where the effects of the terms in the model enter the model additively without interactions (Anon., 2001), unless specified. In CRS (and similarly in SRS) a moving window is applied within climate space (window size dependent on the climatic variable and controlling the smoothness of the function) and response surfaces are evaluated at regularly spaced points (depending on the climate variables). Each point within the window is weighted so that points near the centre of the window are weighed more strongly than those at the edge of the window. The probabilities of occurrence are then calculated using inverse distance weighted means of the observed probabilities of occurrence in climate space in the window (Gavin and Hu, 2005; Huntley *et al.*, 1995; Huntley *et al.*, 2007). CRS have been used successfully to model a variety of species' distributions (Huntley *et al.*, 2004), most notably plants (Gavin and Hu, 2005; Huntley *et al.*, 1995) and birds (Huntley *et al.*, 2006; Huntley *et al.*, 2007). Beering *et al.* (1995) suggest that local regression may be a more robust technique for extrapolation beyond the area within which the model was built than other methods (see Beering *et al.* 1995, p.272).

Each of these three mentioned statistical methods (GLM, GAM and CRS) will be tested to find the appropriate method for modelling the distribution of migrant birds with a view to predicting the likely response of species' ranges to climatic change. Multi-model approaches such as that adopted by Thuiller (2003) are interesting in that they highlight the differences and similarities in models but they also introduce more uncertainty to the results, as well as confusing the reader. It is better is to quantify the uncertainty before providing the results. Moreover, the differences found between methods in such multi-model studies (Thuiller, 2003) are the result of the underlying assumptions of each method and the choice of

predictor variables (Huntley *et al.*, 2007). Here I compared each method with the same set of variables. To ensure the validity of the models, it is also important to consider their conceptual validity – something that using a multi-model approach does not necessarily do – by choosing methods that approximate the form of the expected relationship. For instance GAM and CRS provide more realistic relationships between species and their environment so it is expected that they should do better at least in terms of describing the relationship.

In this section, each method had its predictive ability tested for each species by running 20 70-30 fits and examining the resulting mean AUC and standard deviation. The methods were also projected on to the IBA data set for 12 species (see section 3.1). The most robust method was chosen as a result of these tests. The three methods were further compared to look for any systematic differences by examining simulated prevalence and by examining differences in simulated presence in distinct climatic zones, i.e. biomes. By using biomes as criteria to examine any spatial differences or similarities between outputs one can highlight the power of the methods to relate climate to species' distribution.

3.2.2 Methods

The combinations of variables found through the splitting technique in section 3.1 were used to construct models for all 229 species using three methods – Generalised Additive Models (GAM; see previous section), Generalised Linear Models (GLM) and Climate Response Surface models (CRS). GLM were implemented in R (R Development Core Team, 2006) with a logit link function and a binomial error distribution. Climate Response Surfaces were fitted using a program modified by Brian Huntley (2006a; 2006b) from the original program written by P.J. Bartlein in Fortran code. Window sizes and number of evaluation points (see above for explanation) were different for each variable and in some case also different for the breeding and non-breeding models (see Appendix I).

The fit of the models was quantified with AUC and Kappa (κ). The maximum kappa was found by evaluating κ for all possible threshold probabilities between 0.000 and 1.000 at intervals of 0.001 (Huntley *et al.*, 2007). If two or more probability of occurrence values gave equal maximum kappa, then the lower/lowest of these probabilities of occurrence was taken as the threshold. This threshold probability was then used to convert the probability of occurrence output to presence-absence maps.

Model comparison

Repeated-measures General Linear Models (GLM or one-way ANOVA) on arcsine square-root transformed AUC and Kappa values were performed with Bonferroni comparisons (Field 2005) to compare model goodness-of-fit. In repeated-measures GLM, there is an assumption that the relationship between pairs of experimental conditions is similar; this is called sphericity (Field, 2005). This assumption is tested using Mauchly's test, which tests whether the variances of the differences between conditions are equal. If Mauchly's test indicated that the assumption of sphericity had been violated then either Greenhouse-Geiser or Hynh-Feldt corrections were applied to the degrees of freedom (Field, 2005). Following the advice of Girden (1992) if the estimates of sphericity were less than 0.75 Greenhouse-Geiser correction were used but if the estimates were than greater than 0.75 then Hynh-Feldt was used since at those values the Greenhouse-Geiser correction is too conservative (Field, 2005). These tests are reported in Appendix II.

Effect size was calculated to provide a measure of the magnitude of the observed effect (see Field (2005) for the equations). Overall effect size (ω^2), which is a measure of how much of the total variation in the response variable is due to the independent variables rather than to within group variance, and effect sizes from contrasts (r), which are an estimate of the strength of the factor's effect on the response and relate to the amount of variance explained in the result (Field 2005), are reported. An effect size of 0.1 is low, 0.3 is medium and 0.5 is large (Field, 2005). The prevalence of each species within the study area (breeding and non-breeding) was calculated (as the proportion of grid cells occupied versus the proportion of grid cells non-occupied by the species) and arcsine square root transformed before performing a repeated measures GLM with contrasts comparing the effect of modelling methods against observed prevalence.

To assess how different the model simulations were, the probabilities of occurrence for each species were correlated between modelling methods. The mean correlation coefficient, as well as the standard deviation, was calculated.

To assess whether there was any systematic spatial difference between the simulations, the study area was divided into biomes to reflect differences in 'climatic niche'. The biomes used were those described by Olson *et al.* (2001). They described 14 biomes of which 13 are found in my study area (Figure 3.5). For each species the proportion of cells in their range in each biome was calculated for the observed data and for each of the three methods' simulations. The proportion data were arcsine square root transformed to normalise

the data. A two-way repeated measure ANOVA was performed comparing the effect of biome, method and the interaction of biome and method on prevalence (proportion present per biome).

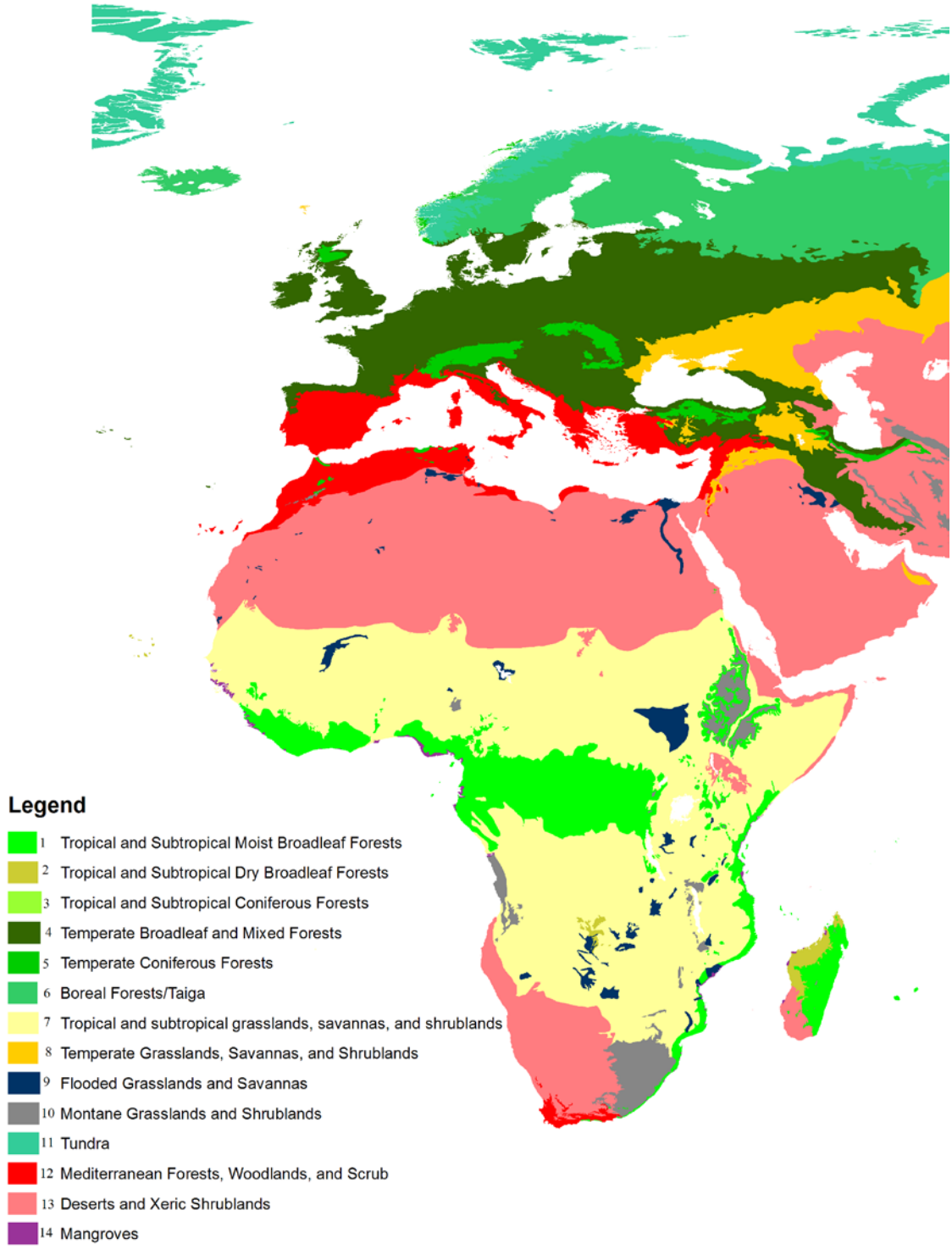


Figure 3.5: Map of the 14 biomes (Olson *et al.*, 2001). In future text, biomes are labelled 1-14 in the above order.

Robustness of each method

To test the robustness of each method, I used the data splitting method as described in section 3.1. Each method was used to run 20 70-30 split data fits. The mean and the standard deviation of each AUC derived from the 20 evaluations were recorded. The frequency of 'best method' from all species, i.e. highest mean AUC with the lowest standard deviation[6], was also recorded. A repeated-measures GLM was performed with Bonferroni comparisons on the mean AUC value per model fit to ascertain which modelling method produced the best predictive fit. The AUC values were arcsine square root transformed prior to the analyses. Log_{10} transformed standard deviations were compared through a repeated-measures GLM.

To test the power of each of the methods on an independent data set, models for 12 species were built using the full data set and projected on to the IBA data set. As discussed in section 3.1.4, this particular means of validation is problematic due to the species selected. However, this test still provides some guidance as to how each method extrapolates. For each method all 10 models and complimentary interaction models (Table 3.2) were constructed and projected. The predicted AUC values were then calculated. A factorial repeated-measure GLM was performed on arcsine square-root transformed AUC values for all models, and for the main 10 models. The null hypothesis is that there is no significant effect of method, model or the interaction between method and model on predictive performance.

3.2.3 Results

Model comparison

The goodness-of-fit of all three methods revealed that CRS produced the best overall fit, followed by GAM and finally GLM (Table 3.7). Maps for all three methods can be found in the digital appendix. These show that CRS most closely fit the observed data. GAM and GLM both over-predict in comparison to the observed data. GLM in particular over-predicts and consequently often produces Kappa values that are worse than random. The spatial aspect of the simulations will be further discussed in section 3.3.

[6] There was always only one choice for the 'best method'

Table 3.7: Descriptive statistics for AUC and Kappa over all species models

	AUC						KAPPA					
	Breeding			Non-breeding			Breeding			Non-breeding		
	GAM	GLM	CRS	GAM	GLM	CRS	GAM	GLM	CRS	GAM	GLM	CRS
MIN	0.798	0.550	0.946	0.812	0.643	0.957	0.213	0.014	0.489	0.111	0.020	0.360
MAX	1.000	0.991	1.000	0.996	0.994	1.000	1.000	0.882	0.955	0.867	0.847	0.933
MEAN	0.953	0.879	0.986	0.943	0.887	0.987	0.680	0.514	0.814	0.584	0.422	0.787

The choice of method affected model performance in terms of AUC on both the breeding and non-breeding grounds (Breeding grounds: $F_{(1.43,\ 327.70)} = 420.129$, $p < 0.0001$, $\omega^2 = 0.448$. Non-breeding grounds: $F_{(1.642,\ 374.29)} = 1168.688$, $p < 0.0001$, $\omega^2 = 0.51$).

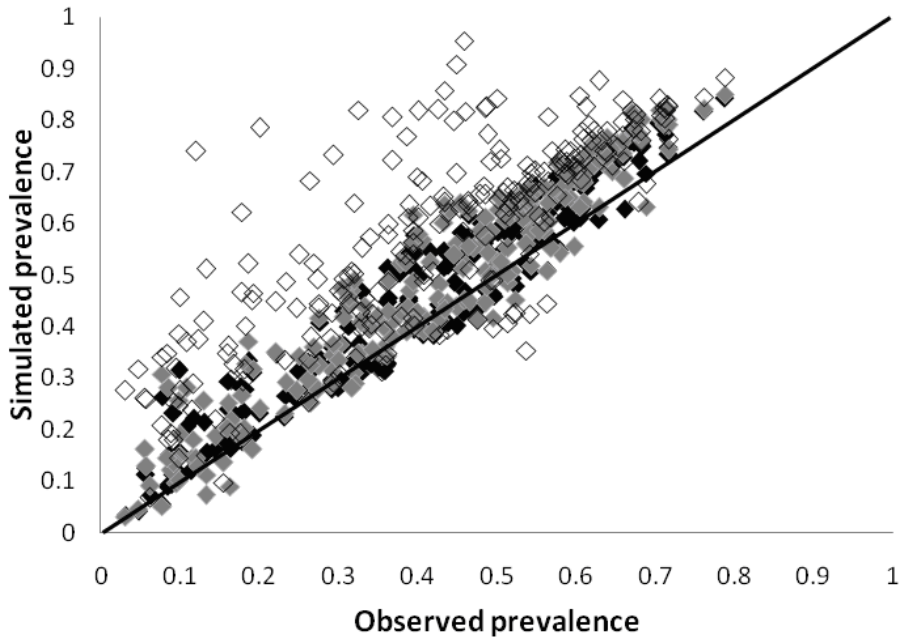
Bonferroni *post hoc* tests showed that all methods performed significantly differently from each other ($p < 0.0001$). Specifically, CRS mean goodness-of-fit was better than GAM and GLM, and GAM was better than GLM. All analyses were also performed on Kappa but the overall results were the same and so not reported here.

The observed and simulated[7] prevalence were all significantly correlated (Fig. 3.6). CRS and GAM were more correlated to each other than with GLM (Fig. 3.6). Prevalence was affected by method and observed data on both the breeding and non-breeding grounds (Breeding grounds: $F_{(1.44,\ 329.51)} = 196.655$, $p < 0.0001$, $\omega^2 = 0.463$. Non-breeding grounds: $F_{(1.27,\ 291.02)} = 132.460$, $p < 0.0001$, $\omega^2 = 0.367$).

Bonferroni *post hoc* tests showed that all methods performed significantly differently from each other on the breeding grounds ($p < 0.0001$) but that CRS did not differ from the observed data on the non-breeding grounds.

[7] The terms simulation, prediction and projection are used interchangeably in this thesis. However, the term simulation is preferred when referring to the outputs of the species distribution model for the present time period and prediction/projection is preferred for the future time period

a)



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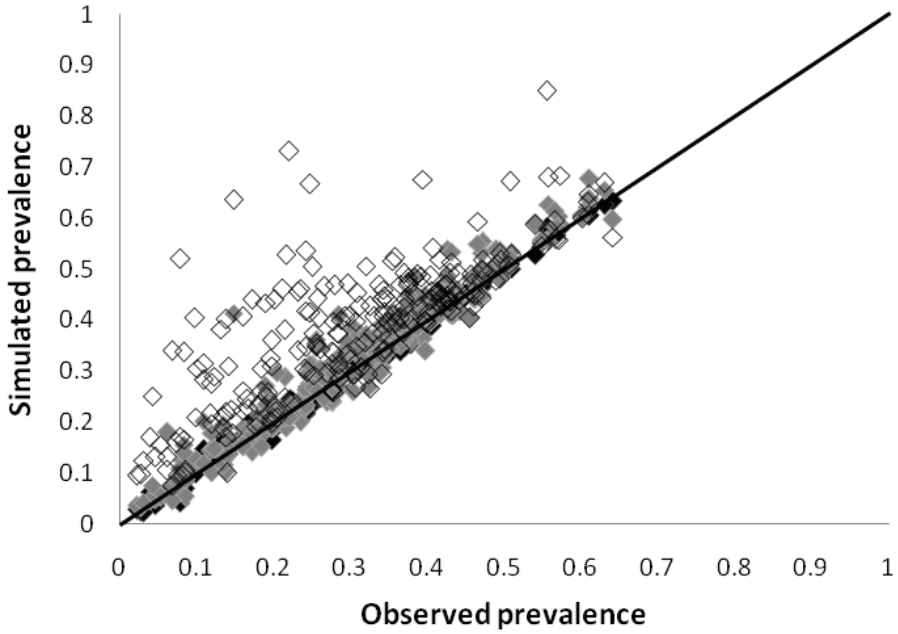


Figure 3.6: Relationship between observed and simulated prevalence including a 1:1 line; The black squares represent the CRS model, grey the GAM model and white the GLM model;a) Breeding ground models. Person correlations CRS: 0.959, GAM: 0.953, GLM: 0.785; b) Non-breeding ground models. Person correlations CRS: 0.996, GAM: 0.968, GLM: 0.977.

The mean correlation as well as standard deviation can be found in Tables 3.8-3.11. These show that there was a greater correlation between GAM and CRS than between the other models.

Table 3.8: Mean correlation coefficients for the breeding range models

Models	GAM	GLM	CRS
GAM	1		
GLM	0.696	1	
CRS	0.851	0.603	1

Table 3.9: Mean standard deviation for breeding models correlation coefficients

Models	GAM	GLM	CRS
GAM	1		
GLM	0.275	1	
CRS	0.105	0.276	1

Table 3.10: Mean correlation coefficients for the non-breeding range models

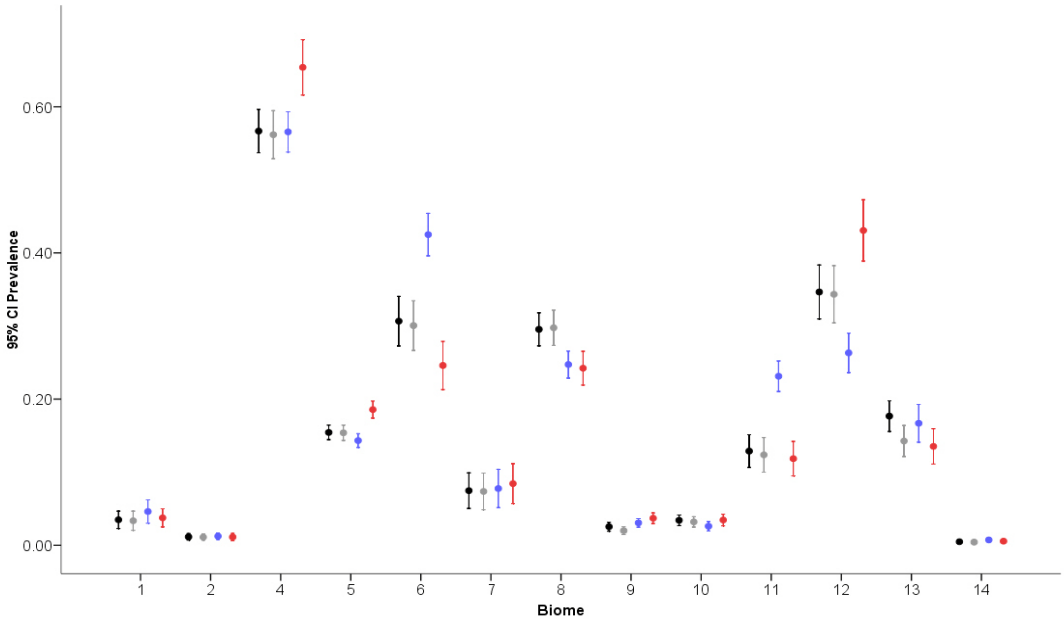
Models	GAM	GLM	CRS
GAM	1		
GLM	0.738	1	
CRS	0.817	0.584	1

Table 3.11: Mean standard deviation for non-breeding models correlation coefficients

Models	GAM	GLM	CRS
GAM	1		
GLM	0.196	1	
CRS	0.116	0.212	1

All effects are reported as significant at $p \leq 0.001$ on the simulated prevalence across biomes (Fig. 3.7). There was a significant effect of biome for both season models ($F_{(3.23,737.1)} = 297.97$, $\omega^2 = 0.567$ for the breeding range and $F_{(2.05,467.52)} = 273.65$, $\omega^2 = 0.546$ for the non-breeding range). There was a significant effect of method for the breeding range ($F_{(2.13,487.36)} = 32.389$, $\omega^2 = 0.124$) and the non-breeding range ($F_{(1.82,416.35)} = 13.97$, $\omega^2 = 0.058$). Contrasts revealed that GLMs' spatial simulations were significantly different from the observed data for both the breeding ($F_{(1,228)} = 43.16$, $r = 0.159$) and non-breeding grounds ($F_{(1,228)} = 11.21$, $r = 0.047$), as was CRS on the breeding grounds ($F_{(1,228)} = 6.64$, $r = 0.028$). However CRS did not produce different simulated prevalence from the observed data on the non-breeding grounds ($F_{(1,228)} = 0.00$, $r = 0$) and GAM was no different on either the breeding grounds ($F_{(1,228)} = 0.722$, $r = 0.003$) or the non-breeding grounds (($F_{(1,228)} = 2.26$, $r = 0.010$). There was also a significant interaction effect between method and biome ($F_{(5.7,1301.3)} = 29.06$, $\omega^2 = 0.115$) on the breeding grounds and on the non-breeding grounds ($F_{(2.95,672.65)} = 6.01$, $\omega^2 = 0.026$). Contrasts revealed that significant differences existed more often between CRS and GLM and GAM and GLM (Fig. 3.7).

a)



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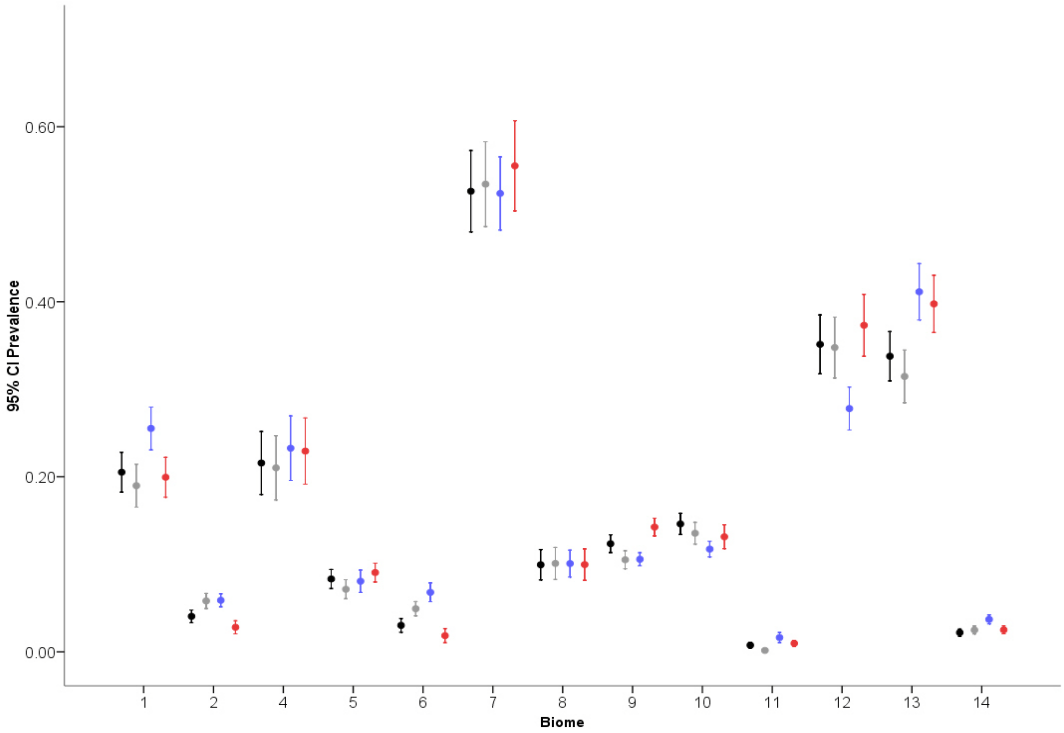


Figure 3.7: Mean and range of confidence interval for the transformed prevalence against biome for each method for a) the breeding models and b) the non-breeding methods. Black = Climate Response Surface, grey = Generalised Additive Models, blue = Generalised Linear Models and red = the Observed Prevalence. See Fig. 3.5 for biome definitions.

Robustness of each method

Table 3.12 shows the average, minimum and maximum Mean AUC and standard deviation for each of the three methods. This shows that on average CRS was better than other methods in terms of the Mean AUC though it also had the lowest Mean AUC of all of the methods.

Table 3.12: Descriptive statistics for the mean AUC and standard deviation produced from the 20 evaluations.

	GAM				GLM				CRS			
	breeding		non-breeding		breeding		non-breeding		breeding		non-breeding	
	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ
MIN	0.824	0.001	0.766	0.001	0.562	0.002	0.664	0.001	0.385	0.001	0.304	0.001
MAX	0.997	0.207	0.996	0.104	0.991	0.091	0.996	0.130	0.999	0.083	0.993	0.201
MEAN	0.950	0.006	0.923	0.008	0.876	0.011	0.862	0.010	0.954	0.008	0.933	0.011

Method affected the predictive performance (Mean AUC) of the models on both the breeding grounds and the non-breeding grounds (breeding grounds: $F_{(1.66, 378.99)} = 247.926$, $p < 0.0001$, $\omega^2 = 0.234$. Non-breeding grounds: $F_{(1.61, 367.2)} = 253.540$, $p < 0.0001$, , $\omega^2 = 0.199$).

Bonferroni *post hoc* tests showed that all methods performed significantly differently from each other ($p < 0.05$). Indeed, CRS mean goodness-of-fit was better than GAM and GLM and GAM was better than GLM. Contrasts showed that the effect size was low between GAM and CRS (breeding r = 0.175, non-breeding r = 0.256) and high between GAM and GLM (breeding r = 0.770, non-breeding r = 0.827) and high between CRS and GLM (breeding r = 0.749, non-breeding r = 0.757).

Method affected the robustness of the predictive performance (standard deviation) on both the breeding grounds and the non-breeding grounds (breeding grounds: $F_{(2, 457)} = 101.686$, $p < 0.0001$, $\omega^2 = 0.089$. Non-breeding grounds: $F_{(1.66, 379.23)} = 58.544$, $p < 0.0001$, $\omega^2 = 0.04$).

Bonferroni *post hoc* tests showed that all methods performed significantly differently from each other ($p < 0.05$). Indeed, GAM standard deviations were lower than both GLM and CRS, and CRS' were lower than GAM (Fig. 3.8). Focused effect size showed that the effect size was low between GAM and CRS (breeding r = 0.248, non-breeding r = 0.236) and high between GAM and GLM (breeding r = 0.702, non-breeding r =0.690) and high to medium between CRS and GLM (breeding r = 0.530, non-breeding r =0.366).

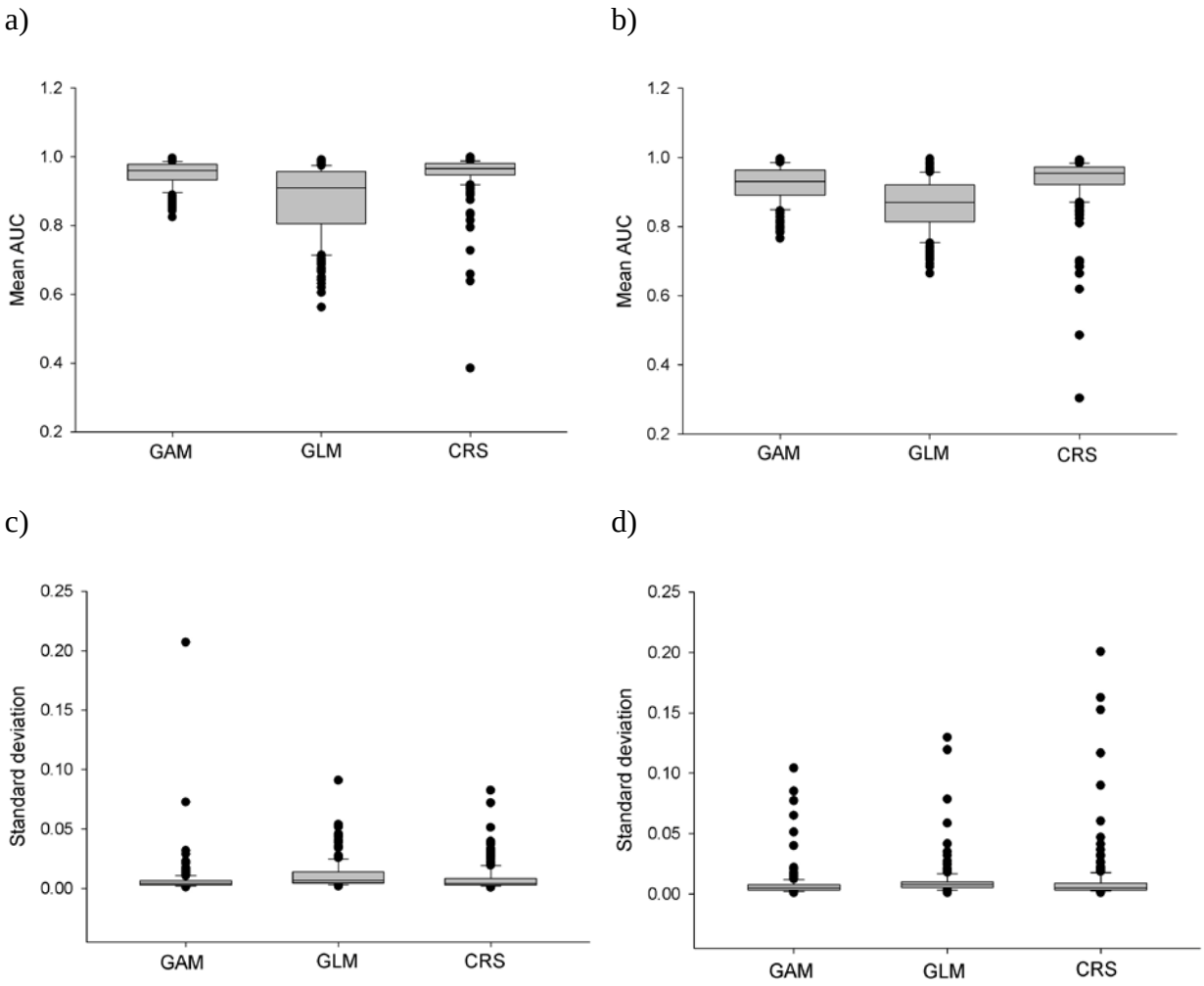


Figure 3.8: Box plots of Mean AUC and standard deviation from the 20 70-30 splits for the 3 modelling approaches; a) and c) breeding models and b) and d) non-breeding models

The actual AUC values produced from the independent validation showed that some of the models' predictive ability was worse than random, i.e. AUC≤ 0.5, but that some were excellent, i.e. AUC≥ 0.9. Excellent models were produced for five out of the 12 species (*C. rufficolis, C. morinellus, P. porzana, L. lapponica* and *S. undata*), whilst good models (AUC = 0.79-0.89) were produced for a further three species (*G. fulvus, P. apivorus* and *L. nubicus*). The independent validation with the IBA data set revealed that GAM and CRS performed similarly but GLM were always worse (Table 3.13, 3.14 and Table 3.4) overall. Figure 3.9a) shows box plots of AUC for each method across all models for the 12 species. Figure 3.10a) shows box plots of AUC for each method and model for the 12 species.

There was a significant effect on predictive performance from method ($F_{(2,22)}$ = 7.01, p < 0.01, ω^2 = 0.392) and from models ($F_{(3.08,33.89)}$ = 3.216 p < 0.05, ω^2 = 0.226) but not from the interaction between methods and models ($F_{(4.49,49.43)}$ = 2.317, p = 0.063, ω^2 = 0.174). The contrasts revealed that GAM and CRS performed no differently from each other ($F_{(1,11)}$ = 4.02, p = 0.07, r = 0.268), GAM and GLM performed no differently from each other ($F_{(1,11)}$ = 4.11, p = 0.068, r = 0.272), but that CRS and GLM were significantly different from each other ($F_{(1,11)}$ = 11.43, p < 0.05, r = 510).

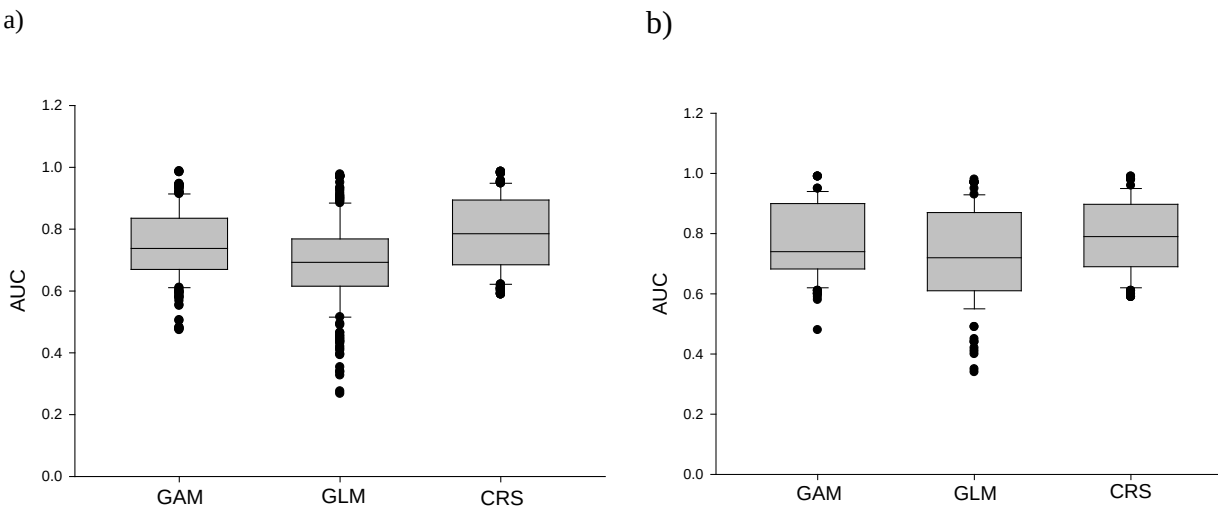


Figure 3.9: Box plots for the AUC_{IBA} from each method for 12 species over a) 20 models (10 models + 10 interaction models) and b) over 10 models (no interactions).

The results were slightly different if interaction models were excluded from the analyses (Fig. 3.9b and 3.10b). There was a significant effect on predictive performance from models ($F_{(3.59,39.25)}$ = 2.929, p < 0.05, ω^2 = 0.210) and from interaction between methods and models ($F_{(4.14,45.56)}$ = 3.081 p < 0.05, ω^2 = 0.219) but not from the different methods ($F_{(4.49,49.43)}$ = 3.144, p = 0.096, ω^2 = 0.222). Contrasts for the interaction between models and methods revealed that significant differences existed more often between CRS and GLM and GAM and GLM.

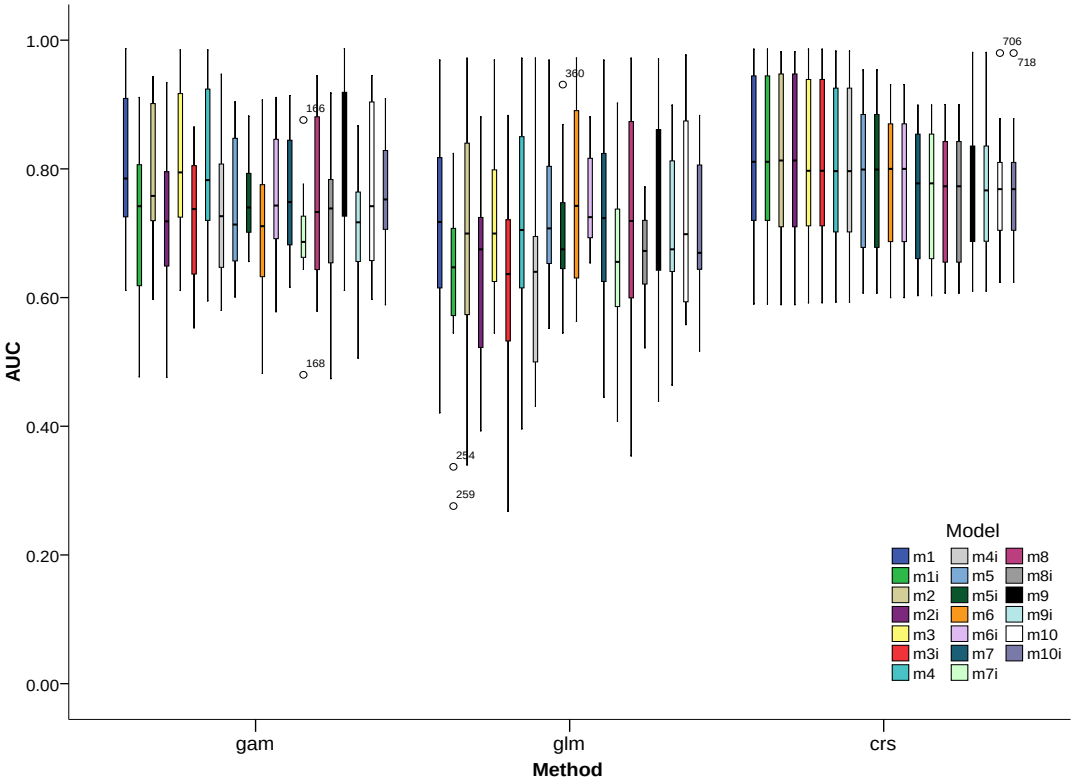
Table 3.13: AUC values from the predictive models (see Table 3.2) on the IBA dataset built using GLM

IBAmodels	*A. nisus*	*G. fulvus*	*P. apivorus*	*C. ruficollis*	*C. morinellus*	*H. rustica*	*L. nubicus*	*P. porzana*	*A. hypoleucos*	*L. lapponica*	*S. communis*	*S. undata*
m1	0.627	0.421	0.715	0.720	0.878	0.603	0.438	0.757	0.725	0.969	0.679	0.885
m1i	0.657	0.337	0.642	0.599	0.545	0.722	0.276	0.723	0.641	0.652	0.693	0.824
m2	0.588	0.414	0.677	0.815	0.873	0.559	0.340	0.735	0.722	0.972	0.642	0.865
m2i	0.657	0.447	0.701	0.393	0.881	0.727	0.516	0.742	0.722	0.654	0.693	0.529
m3	0.637	0.545	0.717	0.838	0.545	0.613	0.679	0.759	0.720	0.969	0.682	0.951
m3i	0.622	0.327	0.649	0.454	0.883	0.611	0.268	0.718	0.724	0.654	0.624	0.809
m4	0.623	0.396	0.694	0.826	0.874	0.607	0.572	0.755	0.716	0.972	0.674	0.934
m4i	0.636	0.435	0.644	0.431	0.545	0.729	0.611	0.671	0.719	0.972	0.658	0.455
m5	0.626	0.701	0.714	0.844	0.696	0.601	0.552	0.764	0.723	0.969	0.680	0.907
m5i	0.657	0.703	0.644	0.869	0.545	0.727	0.565	0.768	0.646	0.654	0.693	0.931
m6	0.589	0.768	0.709	0.924	0.873	0.563	0.600	0.764	0.721	0.972	0.661	0.908
m6i	0.657	0.688	0.710	0.836	0.881	0.727	0.797	0.766	0.723	0.654	0.698	0.852
m7	0.632	0.494	0.714	0.742	0.879	0.618	0.445	0.769	0.733	0.969	0.691	0.893
m7i	0.657	0.465	0.643	0.779	0.545	0.700	0.408	0.775	0.627	0.654	0.698	0.902
m8	0.603	0.560	0.705	0.874	0.873	0.596	0.354	0.773	0.733	0.972	0.681	0.890
m8i	0.657	0.522	0.713	0.688	0.537	0.727	0.596	0.772	0.646	0.648	0.693	0.732
m9	0.609	0.439	0.710	0.844	0.878	0.678	0.490	0.760	0.729	0.971	0.676	0.899
m9i	0.647	0.464	0.674	0.869	0.882	0.634	0.604	0.756	0.733	0.653	0.676	0.899
m10	0.584	0.580	0.674	0.916	0.876	0.558	0.603	0.749	0.723	0.977	0.646	0.873
m10i	0.644	0.517	0.644	0.836	0.883	0.615	0.776	0.688	0.725	0.651	0.651	0.843

Table 3.14: AUC values from the predictive models (see Table 3.2) on the IBA dataset built using CRS

IBAmodels	*A. nisus*	*G. fulvus*	*P. apivorus*	*C. ruficollis*	*C. morinellus*	*H. rustica*	*L. nubicus*	*P. porzana*	*A. hypoleucos*	*L. lapponica*	*S. communis*	*S. undata*
m1	0.669	0.802	0.790	0.928	0.952	0.590	0.940	0.820	0.740	0.986	0.700	0.949
m1i	0.669	0.802	0.790	0.928	0.952	0.590	0.940	0.820	0.740	0.986	0.700	0.949
m2	0.652	0.809	0.785	0.925	0.949	0.589	0.957	0.817	0.746	0.982	0.674	0.946
m2i	0.652	0.809	0.785	0.925	0.949	0.589	0.957	0.817	0.746	0.982	0.674	0.946
m3	0.658	0.784	0.776	0.901	0.947	0.592	0.935	0.810	0.742	0.986	0.681	0.943
m3i	0.658	0.784	0.776	0.901	0.947	0.592	0.935	0.810	0.742	0.986	0.681	0.943
m4	0.652	0.784	0.776	0.900	0.950	0.593	0.913	0.809	0.745	0.983	0.659	0.938
m4i	0.652	0.784	0.776	0.900	0.950	0.593	0.913	0.809	0.745	0.983	0.659	0.938
m5	0.645	0.685	0.785	0.828	0.901	0.607	0.868	0.813	0.722	0.954	0.671	0.929
m5i	0.645	0.685	0.785	0.828	0.901	0.607	0.868	0.813	0.722	0.954	0.671	0.929
m6	0.656	0.693	0.792	0.853	0.887	0.600	0.844	0.808	0.723	0.931	0.681	0.919
m6i	0.656	0.693	0.792	0.853	0.887	0.600	0.844	0.808	0.723	0.931	0.681	0.919
m7	0.621	0.603	0.771	0.855	0.859	0.616	0.830	0.784	0.713	0.853	0.700	0.899
m7i	0.621	0.603	0.771	0.855	0.859	0.616	0.830	0.784	0.713	0.853	0.700	0.899
m8	0.625	0.607	0.770	0.832	0.881	0.607	0.787	0.776	0.699	0.853	0.685	0.900
m8i	0.625	0.607	0.770	0.832	0.881	0.607	0.787	0.776	0.699	0.853	0.685	0.900
m9	0.640	0.736	0.765	0.822	0.897	0.610	0.698	0.794	0.768	0.981	0.677	0.849
m9i	0.640	0.736	0.765	0.822	0.897	0.610	0.698	0.794	0.768	0.981	0.677	0.849
m10	0.652	0.731	0.777	0.822	0.878	0.624	0.769	0.768	0.752	0.980	0.678	0.798
m10i	0.652	0.731	0.777	0.822	0.878	0.624	0.769	0.768	0.752	0.980	0.678	0.798

a)



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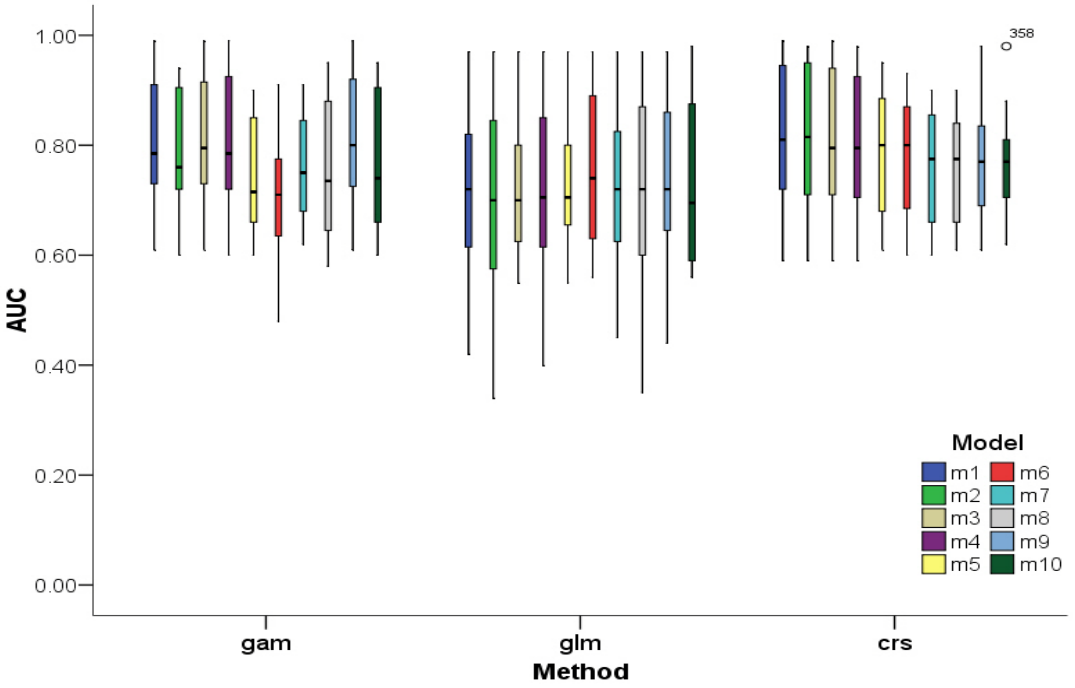

Figure 3.10: Box plots of AUC_{IBA} from each method over each model for 12 species for a) 20 models (10 models + 10 interaction models) and b) 10 models (no interactions).

3.2.4 Discussion

The comparison between all three methods revealed a definite order in model fit: CRS – GAM – GLM. Indeed the method used significantly affected model fit. This was further supported by a large effect size. When dealing with a large number of variables, the strength of the relationship could be significant by chance. Testing the strength of the significance (effect size tests), therefore, gives a better indication of the strength of the relationship (Field 2005). All methods over-predict in some way as is often the case with inductive models (Walther *et al.*, 2007) though CRS simulates prevalence more accurately than the other methods. This is due to its excellent 'curve-fitting' ability. The fact that it locally weights each point and inputs interactions only when necessary makes this method a fine descriptor of the data given. All methods extrapolate as that is part of their purpose: to describe species-climate relationships and apply them over the study area. GLM extrapolates more than the other methods. The differences between GLM's assumptions with the other methods are greater than the differences between GAM and CRS. The worse performance of the GLM may be due to it imposing a linear form to the species-environment relationship, which may not be valid (Barry and Elith, 2006).

The results from the biomes analyses indicate that there may be a slight systematic difference in how the methods simulate species' distribution. The results showed that there were significant effects of both method and the interaction between method and biome. However, these effects were small ($\omega^2 \leq 0.124$). The main effect driving the differences in prevalence is biome, which is expected. The contrasts showed that the effect of method and the interaction was mainly driven by GLM as GAM and CRS were very similar in their simulations as well as to the observed data ($p > 0.05$). GLM showed systematic differences in prevalence in the following biomes: Boreal Forests, Temperate Grassland, Tundra and Mediterranean Forests on the breeding grounds and Tropical Forests, Mediterranean Forests and Desert on the wintering grounds. These differences are due to GLM often over-predicting the prevalence on the non-breeding grounds and under-predicting on the breeding grounds. Non-breeding models constructed for three species of birds have, in previous studies showed similar over-predictions, resulting in these studies clipping the simulated distribution by biomes or ecoregions (Walther *et al.*, 2007; Walther, Wisz and Rahbek, 2004). Under-predicting prevalence on the European breeding grounds by GLM often occurs in models for species that also breed in Africa (see digital appendix). It is possible that the species-climate relationship on the African breeding grounds does not fit linearly with the species-climate relationship on the European breeding grounds, leading GLM to use mostly the African

breeding occurrences, which are more numerous, to build the model. These differences between GLM and the other two methods are due to the fact that GLM focus on general trends in the species' response to environmental predictors whilst the other two methods "give priority to the empirical behaviour" of the species' responses (Segurado and Araújo, 2004). My study is the first, to my knowledge, that has compared model simulations in this way. Errors in simulations are only ever quantified through goodness-of-fit measures which do not show the spatial pattern of these errors (Lobo *et al.*, 2007) or differences. Investigating the spatial differences among predictions is important when the output is intended to be spatial (Barry and Elith, 2006).

The graph plotting observed prevalence against simulated prevalence (Figure 3.6) is interesting for more than its comparison of the different models. It shows that prevalence is, on average, overpredicted on the breeding grounds. This indicates that other factors than climate may be constraining species' distribution. Indeed, Europe is a highly modified landscape so species are not able to occupy all areas that may be climatically suitable.

The results of the comparison between methods based purely on fit would indicate that CRS is the 'best' model in terms of AUC. However, I am concerned with prediction and need to take robustness and generalisability (Vaughan and Ormerod, 2005) into account as well. The tests done on the results from the splitting technique showed that modelling method had a significant effect on predictive performance (mean AUC). However, overall effect size was low, indicating that significance could be due to chance. All methods were different from each other as shown by the Bonferroni comparisons. Effect size of these differences showed that the difference between GLM and the other methods was large ($r > 0.7$) but that the differences between CRS and GAM were low ($r < 0.3$). Method also affected robustness of predictions (standard deviation) and GAM was found to be the most robust method.

Box plots for Mean AUC (Fig. 3.8) showed that although CRS had smaller standard error as well as having a higher mean; its outliers were more spread out than GAM. The standard deviation box plots indicated that CRS may be prone to over-fitting, in contrast to GAM. However, over-fitting is only one aspect limiting generalisability; transferability on to a new data set (independent validation) is the other aspect (Vaughan and Ormerod, 2005).

Independent validation of the methods, performed on all models for 12 species (see section 3.1), indicated that GAM and CRS were similar in their predictive ability. Climate response surface models are slightly different in the way interaction terms are included. In GAM or GLM an interaction term is included in the model. In CRS, the inclusion of an interaction is done locally which allows for more flexibility than having either an interaction or no interaction. In the analyses excluding the interaction models, the choice of method no

longer affected predictive performance, indicating that CRS must not include many interaction terms in its model fitting. Model performance was affected by the interaction between method and model with GLM mostly driving those differences. These results, as well as the comparisons between methods, all point to excluding GLM as a method for modelling the distributions of migratory birds. The results indicate that the response surface is complex and hence requires methods that can model these complexities (Barry and Elith, 2006).

3.2.5 Conclusion

The results of this study are not conclusive with regards to which modelling method to choose. GAM and CRS are very similar, in their assumptions, their way of relating the predictor variables to the response variable, and their simulations. GAM is slightly more robust than CRS, whilst CRS fits the data much better than GAM. The decision on which method to use will involve a trade-off between model accuracy and robustness/generality. The appropriate model is that which has the capabilities that match the objectives of the study (Burgman *et al.*, 2005; Van Horne, 2002). Further, whatever modelling frame chosen, it will always have its shortcomings (Burgman *et al.*, 2005) as "any modelling implementation will include unrealistic biological assumptions, not meet statistical assumptions, omit causal relationships, and/or fail to meet the modelling objective" (Van Horne, 2002, p.69). The decision strategy suggested by Burgman *et al.* (2005) is to seek robust and satisfactory outcomes rather than those that try to maximise performance. GAM have a large evidence base (Guisan *et al.*, 2002) upon which to draw and their strengths and limitations are well established. Moreover, they have been shown in many studies to be robust (Elith *et al.*, 2006; Graham *et al.*, 2007; Guisan *et al.*, 2007; Meynard and Quinn, 2007; Segurado and Araújo, 2004). Climate response surfaces have been applied to a range of species (Huntley *et al.*, 1995; Huntley *et al.*, 2006; Huntley *et al.*, 2004), though their testing in the modelling literature has, until my thesis, been limited. Given the results, I will use both methods to model current species' distributions.

3.3 Species distribution models: current breeding and non-breeding ranges of European-breeding migrant birds

3.3.1 Introduction

Most modelling studies including birds have focused either on their breeding distributions or have included birds as part of a plethora of species (Araújo *et al.*, 2005; Austin *et al.*, 1996; Brotons *et al.*, 2004; Harrison *et al.*, 2003; Huntley *et al.*, 2006; Jetz *et al.*, 2007; Manel *et al.*, 1999; Seoane *et al.*, 2005). Models specifically related to migratory birds are few. Heikkinen *et al.* (2006) modelled the breeding ranges of 63 migratory species breeding in Finland and tailored the models to the migrants by incorporating predictor variables that covered the breeding season rather than annual averages. Two studies model species' winter range, covering three species, to my knowledge (Walther *et al.*, 2007; Walther *et al.*, 2004). This scarcity is due mainly to the quality of the data available.

In this section, I present distribution models for the breeding and non-breeding ranges of European-breeding migrant birds. Only migrant species with most of their breeding ranges in the Western Palaearctic (Europe and North Africa) were considered; therefore this list is not an exhaustive list of European breeding migrants. Species wintering at sea or not wintering in either Europe or Africa were excluded from this study. All values presented are from Generalised Additive Models (GAM) which were shown to be slightly more robust (see section 3.2) than Climate Response Surfaces (CRS). However, CRS results can be found in the digital appendix.

This section also examines how the conceptual model as well as modelling technique used affect the quality of the output. Discrepancies between observed data and simulated data are, however, unavoidable because 1) the simulations are an imperfect model of the data and 2) the data used may not reflect 'reality'. Moreover, some studies suggest that discrepancies in modelling performance may be an ecological artefact rather than a modelling one (McPherson *et al.*, 2004; Seoane *et al.*, 2005). I therefore also investigate whether any ecological factors affect model performance.

3.3.2 Current Simulations

Table 3.15 shows the 229 migrant birds used in this study as well as some ecological information: prevalence, tolerance, biome, habitat and whether the species is a trans-Saharan migrant or not. The habitat specified refers to breeding habitat, which was used because for majority of species non-breeding habitat is similar to breeding habitat (Moreau, 1972). Biome refers to the biome within which the majority of a species' breeding and non-breeding range falls. Seven of the 14 biomes (Fig. 3.5, Olson *et al.*, 2001) are represented as the main biome for the breeding range, and six for the non-breeding range.

Tolerance describes the breadth of a species' niche (Segurado and Araújo, 2004), i.e. how confined it is to a particular climate space. A species is therefore either a climatic specialist, having 80% or more of its range in one biome, or a climatic generalist, its range spanning different biomes. Table 3.15 also includes the conceptual model chosen for each species (see Section 3.1) and the goodness-of-fit (AUC) of each simulation run with GAM (see Section 3.2). Maps of all species with their associated goodness-of-fit measures (AUC and Kappa values) can be found in the digital appendix.

Table 3.15: Results from the modelling as well as ecological information of the European migrants in this study. For "model" definition, refer to Table 3.2, for "Biome" refers to Fig. 3.5. "Tolerance" of 2 is defined for those species where ≥ 80% of their distribution falls within a single biome and "tolerance" of 1 everything else. Habitat categorisation is drawn from Snow and Perrins (1998).

	Breeding					Non-breeding						Trans-
Species	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Saharan
Accipiter nisus	M9	0.976	4	0.379	1	M8	0.903	4	0.400	1	Forest	Y
Acrocephalus arundinaceus	M7	0.979	4	0.282	1	M4	0.986	7	0.102	1	Wetland	Y
Acrocephalus paludicola	M9	0.979	4	0.010	2	M1	0.987	7	0.001	1	Wetland	Y
Acrocephalus palustris	M10	0.965	4	0.233	1	M2i	0.985	7	0.019	1	Wetland	Y
Acrocephalus schoenobaenus	M6	0.933	4	0.297	1	M3	0.990	7	0.130	1	Scrub	Y
Acrocephalus scirpaceus	M7	0.978	4	0.303	1	M8	0.982	7	0.078	1	Wetland	Y
Actitis hypoleucos	M9	0.967	4	0.320	1	M7	0.943	7	0.212	1	Wetland	Y
Alauda arvensis	M10	0.982	4	0.442	1	M8	0.946	12	0.193	1	Open habitat	N
Anas acuta	M9	0.941	6	0.100	1	M8i	0.864	7	0.158	1	Wetland	Y
Anas clypeata	M3	0.927	4	0.188	1	M8i	0.847	12	0.121	1	Wetland	Y
Anas crecca	M5	0.973	4	0.257	1	M8	0.843	4	0.180	1	Wetland	Y
Anas penelope	M5	0.987	6	0.132	1	M8i	0.838	13	0.157	1	Coastal	N
Anas platyrhynchos	M9	0.987	4	0.479	1	M8i	0.895	4	0.209	1	Wetland	N
Anas querquedula	M3	0.957	4	0.234	1	M1i	0.932	7	0.081	1	Wetland	Y
Anthropoides virgo	M10	0.987	8	0.010	2	M1	0.870	12	0.055	1	Open habitat	Y
Anthus campestris	M9	0.996	4	0.236	1	M4i	0.968	7	0.051	1	Open habitat	Y
Anthus cervinus	M1	0.988	11	0.014	1	M4i	0.928	7	0.094	1	Open habitat	Y
Anthus pratensis	M9	0.927	4	0.259	1	M8	0.955	12	0.161	1	Open habitat	N
Anthus spinoletta	M9	0.964	4	0.085	1	M7	0.927	12	0.128	1	Montane	N
Anthus trivialis	M9	0.989	4	0.354	1	M2i	0.984	7	0.083	1	Forest	Y
Apus affinis	M9	0.974	7	0.157	1	M4	0.979	7	0.137	1	Open habitat	Y
Apus Apus	M3	0.973	4	0.478	1	M3	0.981	7	0.078	1	Open habitat	Y

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	Breeding					Non-breeding						
Table 3.15 continued	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Trans-Saharan
Apus pallidus	M9	0.929	12	0.085	1	M3	0.926	7	0.022	1	Open habitat	Y
Aquila clanga	M4	0.972	4	0.010	1	M4	0.850	13	0.061	1	Forest	Y
Aquila heliaca	M4	0.945	4	0.033	1	M4	0.825	13	0.059	1	Open habitat	Y
Aquila nipalensis	M9	1.000	8	0.003	1	M4	0.993	8	0.006	1	Open habitat	Y
Aquila pomarina	M10	0.952	4	0.076	2	M4	0.993	7	0.026	2	Open habitat	Y
Ardea cinerea	M3	0.895	4	0.457	1	M8	0.922	7	0.316	1	Wetland	Y
Ardea purpurea	M3	0.955	7	0.268	1	M1i	0.986	7	0.159	1	Wetland	Y
Ardeola ralloides	M3	0.961	7	0.225	1	M4	0.981	7	0.162	1	Wetland	Y
Arenaria interpres	M9	0.996	6	0.010	1	M8	0.902	12	0.041	1	Coastal	Y
Asio flammeus	M4	0.935	4	0.156	1	M2i	0.896	4	0.114	1	Open habitat	Y
Asio otus	M9	0.947	4	0.340	1	M8	0.954	4	0.255	1	Forest	N
Aythya ferina	M3	0.948	4	0.221	1	M8i	0.863	12	0.165	1	Wetland	N
Aythya fuligula	M5	0.974	4	0.250	1	M4i	0.879	4	0.149	1	Wetland	N
Aythya nyroca	M4	0.952	4	0.055	1	M7	0.842	7	0.092	1	Wetland	Y
Botaurus stellaris	M9	0.798	7	0.253	1	M7	0.832	7	0.147	1	Wetland	Y
Bubulcus ibis	M9	0.956	7	0.272	1	M7	0.965	7	0.220	1	Open habitat	N
Burhinus oedicnemus	M7	0.881	12	0.261	1	M3	0.942	13	0.320	1	Open habitat	Y
Buteo buteo	M3	0.981	4	0.297	1	M7	0.937	4	0.305	1	Open habitat	Y
Buteo rufinus	M3	0.938	12	0.165	1	M7	0.913	13	0.155	1	Open habitat	N
Calandrella brachydactyla	M8	0.939	12	0.234	1	M3	0.921	13	0.140	1	Open habitat	Y
Calidris alpina	M9	0.997	4	0.069	1	M7	0.869	12	0.050	1	Coastal	N
Calidris minuta	M1	0.991	11	0.003	2	M7	0.962	7	0.201	1	Coastal	Y
Calidris temminckii	M2	0.982	11	0.027	1	M1	0.942	7	0.077	1	Wetlands	Y
Caprimulgus europaeus	M7	0.950	4	0.367	1	M7	0.963	7	0.036	1	Open habitat	Y
Caprimulgus ruficollis	M10	0.980	12	0.054	2	M4i	0.988	7	0.005	1	Open habitat	Y
Carduelis cannabina	M10	0.987	4	0.391	1	M8i	0.967	4	0.361	1	Scrub	N

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	Breeding					Non-breeding						
Table 3.15 continued	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Trans-Saharan
Carduelis carduelis	M8	0.984	4	0.422	1	M7i	0.968	4	0.355	1	Forest	N
Carduelis chloris	M10	0.985	4	0.436	1	M7i	0.959	4	0.365	1	Forest	N
Carpospiza brachydactyla	M10	0.924	12	0.002	1	M1i	0.963	13	0.002	1	Montane	N
Cercotrichas galactotes	M7	0.987	12	0.130	1	M4	0.990	7	0.031	1	Human	Y
Cettia cetti	M9	0.946	12	0.215	1	M8	0.968	12	0.118	1	Scrub	N
Charadrius alexandrinus	M10	0.875	12	0.092	1	M7	0.874	13	0.141	1	Coastal	Y
Charadrius dubius	M7	0.930	4	0.422	1	M8	0.957	7	0.133	1	Wetland	Y
Charadrius hiaticula	M6	0.976	4	0.128	1	M3	0.959	7	0.208	1	Coastal	Y
Charadrius morinellus	M9	0.978	11	0.029	1	M8	0.962	12	0.039	1	Montane	N
Childonias niger	M3	0.919	4	0.116	1	M1i	0.922	12	0.042	1	Coastal	Y
Chlidonais hybridus	M10	0.983	7	0.087	1	M8	0.909	7	0.186	1	Coastal	Y
Chlidonias leucopterus	M4	0.916	4	0.037	1	M3	0.947	7	0.220	1	Coastal	Y
Cicaetus gallicus	M9	0.937	12	0.211	1	M4	0.989	7	0.026	2	Open habitat	Y
Ciconia ciconia	M9	0.860	4	0.386	1	M8	0.931	7	0.173	1	Open habitat	Y
Ciconia nigra	M9	0.832	4	0.236	1	M3	0.929	7	0.117	1	Forest	Y
Circus aeruginosus	M9	0.936	4	0.262	1	M8	0.917	7	0.143	1	Wetlands	Y
Circus cyaneus	M3	0.943	4	0.164	1	M7	0.946	4	0.180	1	Open habitat	N
Circus macrourus	M10	0.985	8	0.007	1	M7	0.932	7	0.098	1	Open habitat	Y
Circus pygargus	M3	0.905	4	0.192	1	M4i	0.979	7	0.076	1	Open habitat	Y
Clamator glandarius	M3	0.946	7	0.176	1	M3i	0.969	7	0.082	1	Human	Y
Coccothraustes coccothraustes	M9	0.967	4	0.293	1	M8	0.968	4	0.221	1	Forest	N
Columba palumbus	M10	0.973	4	0.449	1	M7	0.967	12	0.126	1	Forest	N
Coracias garrulus	M10	0.950	4	0.201	1	M3	0.965	7	0.086	1	Forest	Y
Coturnix coturnix	M10	0.964	4	0.338	1	M7	0.913	7	0.147	1	Open habitat	Y
Crex crex	M4	0.941	4	0.214	1	M7	0.896	7	0.117	1	Open habitat	Y
Cuculus canorus	M10	0.989	4	0.490	1	M4	0.989	7	0.096	1	Open habitat	Y

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	Breeding					Non-breeding						
Table 3.15 continued	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Trans-Saharan
Delichon urbica	M5	0.980	4	0.487	1	M3	0.964	7	0.137	1	Open habitat	Y
Egretta alba	M9	0.963	7	0.243	1	M7	0.952	7	0.206	1	Wetland	Y
Egretta garzetta	M3	0.844	7	0.244	1	M7	0.918	7	0.190	1	Wetland	Y
Embeiza cia	M9	0.932	12	0.181	1	M8	0.939	12	0.119	1	Scrub	N
Emberiza caesia	M3	0.975	12	0.037	2	M3	0.993	7	0.004	2	Open habitat	N
Emberiza cineracea	M3	0.990	12	0.009	1	M1	0.995	13	0.001	1	Scrub	N
Emberiza hortulana	M10	0.932	4	0.251	1	M1i	0.964	7	0.007	1	Forest	Y
Emberiza schoeniclus	M9	0.975		0.337	1	M8	0.953	4	0.179	1	Wetland	N
Erithacus rubecula	M7	0.984	4	0.421	1	M8	0.942	4	0.207	1	Forest	Y
Falco cherrug	M9	0.969	4	0.032	1	M4i	0.842	13	0.072	1	Open habitat	Y
Falco columbarius	M6	0.991	6	0.098	1	M8	0.942	4	0.221	1	Open habitat	N
Falco eleonorae	M9	0.961	12	0.013	2	M1i	0.990	1	0.010	1	Coastal	Y
Falco naumanni	M9	0.963	12	0.136	1	M1i	0.981	7	0.174	1	Open habitat	Y
Falco peregrinus	M9	0.877	12	0.199	1	M6	0.894	4	0.364	1	Open habitat	Y
Falco subbuteo	M9	0.961	4	0.359	1	M2	0.992	7	0.041	1	Open habitat	Y
Falco tinnunculus	M9	0.940	4	0.583	1	M7	0.899	4	0.387	1	Open habitat	Y
Falco vespertinus	M4	0.982	4	0.049	1	M3	0.988	7	0.020	1	Open habitat	Y
Ficedula albicollis	M10	0.955	4	0.073	1	M4	0.992	7	0.014	2	Open forest	Y
Ficedula hypoleuca	M10	0.958	4	0.263	1	M1	0.991	7	0.028	1	Forest	Y
Ficedula semitorquata	M9	0.971	4	0.015	1	M4	0.996	7	0.007	1	Forest	Y
Fringilla coelebs	M8	0.986	4	0.488	1	M8	0.953	4	0.242	1	Forest	N
Gallinago gallinago	M6	0.974	4	0.274	1	M3	0.905	7	0.215	1	Wetland	Y
Gallinago media	M1	0.933	4	0.035	1	M3	0.951	7	0.078	1	Wetland	Y
Gallinula chloropus	M4	0.950	4	0.350	1	M3i	0.877	13	0.034	1	Wetland	Y
Gelochelidon nilotica	M4	0.843	12	0.024	1	M7	0.889	7	0.093	1	Coastal	Y
Geronticus ermita	M10	0.845	12	0.007	2	M4	0.939	13	0.067	1	Open habitat	Y

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	Breeding					Non-breeding						
Table 3.15 continued	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Trans-Saharan
Glareola praticola	M9	0.870	7	0.071	1	M2i	0.966	7	0.095	1	Scrub	Y
Grus grus	M10	0.978	4	0.142	1	M2	0.819	12	0.062	1	Open habitat	Y
Gyps fulvus	M9	0.922	12	0.102	1	M3	0.812	12	0.063	1	Montane	N
Hieraaetus pennatus	M10	0.945	12	0.144	1	M3	0.978	7	0.118	1	Forest	Y
Himantopus himantopus	M3	0.897	7	0.261	1	M7	0.932	7	0.170	1	Wetlands	Y
Hippolais icterina	M4	0.972	4	0.228	1	M8	0.988	7	0.045	1	Forest	Y
Hippolais languidae	M4	0.858	4	0.167	1	M3	0.996	7	0.006	1	Open habitat	Y
Hippolais pallida	M9	0.961	12	0.209	1	M8	0.919	7	0.105	1	Scrub	Y
Hippolais polyglotta	M9	0.986	12	0.126	1	M1	0.992	7	0.018	1	Forest	Y
Hirundo daurica	M3	0.921	12	0.090	1	M3	0.966	7	0.015	1	Open habitat	Y
Hirundo rupestris	M9	0.934	12	0.160	1	M2i	0.887	12	0.068	1	Montane	Y
Hirundo rustica	M8	0.981	4	0.548	1	M3	0.967	7	0.127	1	Open habitat	Y
Irania gutturalis	M9	0.967	12	0.032	1	M2i	0.996	7	0.002	2	Montane	Y
Ixobrychus minutus	M3	0.892	7	0.290	1	M4	0.961	7	0.133	1	Wetland	Y
Jynx torquilla	M9	0.939	4	0.341	1	M8	0.978	7	0.058	1	Forest	Y
Lanius collurio	M8	0.925	4	0.363	1	M8	0.980	7	0.047	1	Open habitat	Y
Lanius minor	M9	0.979	13	0.151	1	M4i	0.955	13	0.030	1	Open habitat	Y
Lanius nubicus	M3	0.954	12	0.032	1	M4i	0.974	7	0.014	1	Forest	Y
Lanius senator	M9	0.983	12	0.182	1	M4i	0.966	7	0.076	1	Forest	Y
Larus fuscus	M5	0.956	4	0.086	1	M8	0.904	7	0.021	1	Coastal	Y
Larus genei	M4	0.950	4	0.018	1	M2i	0.940	12	0.012	1	Coastal	Y
Larus ridibundus	M5	0.979	4	0.287	1	M8	0.906	4	0.126	1	Wetland	Y
Limicola falcinellus	M9	0.997	6	0.026	2	M3	0.993	13	0.000	1	Wetland	N
Limosa lapponica	M9	0.975	11	0.008	1	M8	0.933	12	0.019	1	Coastal	N
Limosa limosa	M4	0.992	4	0.109	1	M8	0.958	7	0.187	1	Coastal	Y
Locustella fluviatilis	M4	0.928	4	0.132	2	M4	0.993	7	0.010	2	Scrub	Y

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	Breeding					Non-breeding						
Table 3.15 continued	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Trans-Saharan
Locustella lusciniodes	M10	0.973	4	0.151	1	M2	0.985	7	0.005	1	Wetland	Y
Locustella naevia	M3	0.929	4	0.208	2	M3i	0.962	12	0.006	1	Scrub	Y
Lullula arborea	M3	0.959	4	0.345	1	M8	0.953	12	0.109	1	Open habitat	N
Luscina megarhynchos	M9	0.987	4	0.291	1	M3	0.988	7	0.037	1	Forest	Y
Luscinia luscinia	M10	0.862	4	0.156	1	M3	0.993	7	0.012	2	Forest	Y
Luscinia svecica	M5	0.917	4	0.161	1	M4	0.880	7	0.071	1	Scrub	Y
Lymnocryptes minimus	M1	0.961	6	0.033	2	M3	0.910	7	0.116	1	Wetland	Y
Marmaronetta angustirostris	M3	0.944	12	0.021	1	M3	0.928	12	0.019	1	Wetland	Y
Melanocorypha bimaculata	M10	0.984	4	0.031	1	M1i	0.957	13	0.007	1	Human	N
Melanocorypha calandra	M8	0.963	12	0.182	1	M8i	0.966	12	0.135	1	Open habitat	N
Merops apiaster	M8	0.941	12	0.249	1	M1i	0.982	7	0.018	2	Open habitat	Y
Miliaria calandra	M10	0.973	4	0.364	1	M8	0.943	4	0.220	1	Open habitat	N
Milvus migrans	M9	0.918	7	0.446	1	M3	0.967	7	0.194	1	Open habitat	Y
Milvus milvus	M9	0.915	4	0.123	1	M8	0.934	12	0.046	1	Open habitat	N
Monticola saxatilis	M9	0.952	12	0.106	1	M2i	0.966	7	0.026	1	Montane	Y
Monticola solitarius	M9	0.972	12	0.159	1	M3	0.874	12	0.102	1	Montane	Y
Motacilla alba	M9	0.945	4	0.486	1	M7	0.856	13	0.304	1	Wetland	Y
Motacilla cinerea	M9	0.962	4	0.289	1	M8	0.932	13	0.184	1	Wetland	Y
Motacilla flava	M9	0.987	4	0.437	1	M3	0.979	7	0.152	1	Open habitat	Y
Muscicapa striata	M7	0.976	4	0.451	1	M8	0.968	7	0.116	1	Forest	Y
Neophron percnopterus	M9	0.865	12	0.233	1	M3	0.942	7	0.090	1	Montane	Y
Netta rufina	M9	0.885	4	0.040	1	M3	0.837	13	0.059	1	Wetland	N
Numenicus arquata	M9	0.992	4	0.187	1	M3	0.873	12	0.065	1	Coastal	Y
Numenicus phaeopus	M7	0.973	6	0.076	1	M7	0.948	7	0.039	1	Coastal	Y
Nycticorax nycticorax	M3	0.844	7	0.240	1	M7	0.916	7	0.150	1	Wetland	Y
Oenanthe hispanica	M9	0.984	12	0.187	1	M3	0.944	7	0.064	1	Open habitat	Y

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	Breeding					Non-breeding						
Table 3.15 continued	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Trans-Saharan
Oenanthe isabellina	M3	0.972	8	0.069	1	M4i	0.939	7	0.081	1	Open habitat	Y
Oenanthe oenanthe	M9	0.979	4	0.439	1	M4i	0.925	7	0.105	1	Montane	Y
Oenanthe pleschanka	M9	0.991	8	0.017	1	M4i	0.970	7	0.039	1	Scrub	Y
Oenanthe xanthoprymna	M9	0.962	8	0.004	1	M1	0.946	13	0.006	2	Montane	Y
Oriolus oriolus	M9	0.929	4	0.364	1	M8	0.973	7	0.077	1	Forest	Y
Otus scops	M9	0.964	12	0.285	1	M8	0.978	7	0.123	1	Forest	Y
Pandion haliaetus	M3	0.987	6	0.094	1	M7	0.967	7	0.184	1	Wetland	Y
Passer hispaniolensis	M9	0.977	12	0.201	1	M4	0.958	13	0.180	1	Scrub	N
Passer montanus	M9	0.991	4	0.327	1	M4	0.972	4	0.323	1	Forest	N
Pelecanus onocrotatus	M9	0.956	7	0.156	1	M3	0.938	7	0.154	1	Wetland	N
Pernis apivorus	M1	0.954	4	0.276	1	M7	0.943	7	0.240	1	Forest	Y
Philomachus pugnax	M9	0.997	6	0.102	1	M7	0.963	7	0.181	1	Open habitat	Y
Phoenicurus ochruros	M9	0.970	4	0.318	1	M8	0.935	12	0.137	1	Human	Y
Phoenicurus phoenicurus	M9	0.980	4	0.375	1	M4i	0.974	7	0.047	1	Forest	Y
Phylloscopus bonelli	M9	0.982	12	0.128	1	M3	0.967	7	0.034	1	Forest	Y
Phylloscopus collybita	M9	0.985	4	0.399	1	M4	0.868	13	0.306	1	Forest	Y
Phylloscopus sibilatrix	M9	0.988	4	0.288	1	M2	0.994	1	0.032	1	Forest	Y
Phylloscopus trochilus	M9	0.985	4	0.290	1	M3	0.977	7	0.108	1	Scrub	Y
Platalea leucorodia	M3	0.939	12	0.108	1	M3	0.904	13	0.081	1	Wetland	Y
Plefadis falcinellus	M9	0.938	7	0.313	1	M4	0.954	7	0.243	1	Wetland	Y
Pluvialis apricaria	M7	0.989	6	0.111	1	M8	0.925	12	0.065	1	Montane	N
Podiceps cristatus	M9	0.889	4	0.266	1	M7	0.923	4	0.122	1	Wetland	N
Podiceps nigricollis	M9	0.902	4	0.135	1	M8	0.919	12	0.088	1	Wetland	N
Porzana parva	M4	0.954	4	0.063	1	M3	0.977	13	0.003	1	Wetland	Y
Porzana porzana	M3	0.899	4	0.173	1	M8	0.951	7	0.054	1	Wetland	Y
Porzana pusilla	M3	0.947	1	0.027	1	M3	0.990	7	0.066	1	Wetland	Y

	Breeding					Non-breeding						
Table 3.15 continued	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Trans-Saharan
Prunella modularis	M9	0.964	4	0.326	1	M8	0.960	4	0.163	1	Forest	N
Rallus aquaticus	M3	0.890	4	0.310	1	M8	0.916	12	0.164	1	Wetland	N
Recurvirostra avosetta	M9	0.956	4	0.070	1	M7	0.939	7	0.140	1	Coastal	Y
Regulus ignicapillus	M9	0.979	4	0.191	1	M7	0.952	12	0.095	1	Forest	N
Regulus regulus	M7	1.000	4	0.265	1	M7	0.967	4	0.297	1	Forest	N
Riparia riparia	M6	0.951	4	0.398	1	M7	0.977	7	0.089	1	Open habitat	Y
Saxicola rubetra	M9	0.953	4	0.352	1	M4	0.975	7	0.037	1	Open habitat	Y
Saxicola torquata	M9	0.989	4	0.314	1	M7	0.890	12	0.255	1	Open habitat	N
Scolopax rusticola	M10	0.953	4	0.270	1	M8	0.953	12	0.088	1	Forest	N
Serinus serinus	M9	0.961	4	0.330	1	M8	0.959	12	0.105	1	Forest	N
Sterna albifrons	M9	0.878	4	0.094	1	M6	0.900	12	0.022	1	Coastal	Y
Sterna caspia	M9	0.935	13	0.018	1	M1	0.867	7	0.076	1	Coastal	Y
Sterna hirundo	M6	0.940	4	0.206	1	M2	0.943	12	0.004	1	Coastal	Y
Sterna sandvicensis	M4	0.938	8	0.008	1	M2i	0.981	13	0.002	1	Coastal	Y
Streptopelia turtur	M9	0.935	4	0.492	1	M3i	0.979	7	0.040	1	Forest	Y
Sturnus vulgaris	M7	0.937	4	0.413	1	M6	0.935	4	0.256	1	Open habitat	N
Sylvia artricapilla	M9	0.979	4	0.314	1	M8	0.929	12	0.172	1	Forest	Y
Sylvia borin	M9	0.956	4	0.338	1	M7	0.983	7	0.098	1	Forest	Y
Sylvia cantillans	M3	0.981	12	0.116	2	M3	0.975	7	0.038	1	Scrub	Y
Sylvia communis	M3	0.978	4	0.406	1	M3	0.975	7	0.080	2	Forest	Y
Sylvia conspicillata	M10	0.997	12	0.061	2	M3	0.936	12	0.059	1	Scrub	N
Sylvia curruca	M3	0.936	4	0.309	1	M3	0.949	7	0.040	1	Forest	Y
Sylvia deserticola	M3	0.979	12	0.010	2	M3	0.939	13	0.033	1	Scrub	N
Sylvia hortensis	M3	0.966	12	0.107	1	M1	0.991	7	0.028	1	Forest	Y
Sylvia melanocephala	M3	0.973	12	0.131	2	M3i	0.932	12	0.133	1	Open habitat	Y
Sylvia melanothorax	M3	0.983	12	0.001	2	M1i	0.973	13	0.007	2	Scrub	N

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	Breeding					Non-breeding						
Table 3.15 continued	Model	AUC	Biome	Prevalence	Tolerance	Model	AUC	Biome	Prevalence	Tolerance	Habitat	Trans-Saharan
Sylvia nana	M9	0.947	13	0.008	2	M1	0.953	13	0.007	2	Scrub	Y
Sylvia nisoria	M4	0.985	4	0.132	1	M3	0.973	7	0.018	1	Scrub	Y
Sylvia rueppelli	M4	0.949	12	0.015	2	M1	0.938	13	0.014	1	Scrub	Y
Sylvia sarda	M10	0.982	12	0.006	2	M3	0.977	12	0.010	2	Scrub	N
Sylvia undata	M3	0.970	12	0.085	1	M4	0.978	12	0.064	1	Scrub	N
Tachybaptus ruficollis	M9	0.986	4	0.424	1	M7	0.921	7	0.289	1	Wetland	N
Tachymarptis melba	M9	0.899	12	0.149	1	M3	0.973	1	0.019	1	Open habitat	Y
Tadorna ferruginea	M7	0.845	13	0.118	1	M8i	0.892	13	0.076	1	Wetland	N
Tadorna tadorna	M3	0.921	4	0.103	1	M8i	0.920	4	0.034	1	Wetland	N
Tringa erythropus	M9	0.990	6	0.026	2	M8	0.923	7	0.118	1	Coastal	Y
Tringa glareola	M9	0.994	6	0.098	1	M7	0.974	7	0.174	1	Forest	Y
Tringa nebularia	M7	0.982	6	0.076	1	M7	0.964	7	0.184	1	Open habitat	Y
Tringa ochropus	M10	0.980	4	0.156	1	M8	0.937	7	0.243	1	Wetland	Y
Tringa stagnatilis	M9	0.929	4	0.012	1	M3	0.974	7	0.174	1	Wetland	Y
Tringa totanus	M9	0.994	4	0.240	1	M7	0.953	7	0.211	1	Wetland	Y
Troglodytes troglodytes	M3	0.981	4	0.360	1	M8	0.982	8	0.054	1	Open habitat	N
Turdus iliacus	M9	0.985	4	0.148	1	M7	0.949	4	0.169	1	Forest	N
Turdus merula	M9	0.990	4	0.492	1	M7	0.948	4	0.237	1	Scrub	N
Turdus philomelos	M9	0.988	4	0.379	1	M7	0.939	12	0.166	1	Forest	N
Turdus pilaris	M9	0.950	4	0.215	1	M7	0.956	4	0.317	1	Forest	N
Turdus torquatus	M9	0.966	4	0.101	1	M7	0.941	12	0.049	1	Montane	N
Turdus viscivorus	M9	0.950	4	0.372	1	M7	0.963	4	0.186	1	Forest	N
Upupa epos	M9	0.915	4	0.359	1	M1i	0.914	12	0.136	1	Forest	Y
Vanellus vanellus	M5	0.954	4	0.395	1	M8	0.929	12	0.117	1	Human	N
Xenus cinereus	M9	0.973	4	0.006	1	M3	0.963	7	0.058	1	Wetland	Y

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Predictor variables

The main predictor variables used in this study are depicted in Figures 3.11-13. The base variables, actual/potential evapo-transpiration (APET), mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA) or annual temperature sum above 5ºC (GDD5) were chosen because they were thought to characterise the environment (Huntley *et al.*, 1995; Huntley *et al.*, 2004). The majority of models selected for the breeding range included the difference of precipitation to potential evapo-transpiration (PPE) during the breeding season. The non-breeding range models mainly include either PPE before the non-breeding season or the dry intensity variable (DRYINT) (see Section 3.1). This selection of variables for migratory birds makes sense and concurs with the conclusion by Heikkinen *et al.* (2006) that the inclusion of seasonal variables in models for migratory species improves fit. During the breeding season, available moisture is important for plant productivity, which can help successful breeding through provision of enough food. During the non-breeding season, ensuring that birds arrive in a 'lush' environment may also be important (Fry, 1992). The inclusion of seasonal variables in the non-breeding season models may be more difficult. It has been shown that many migrants are vagrants throughout their non-breeding range, often following the rain (Berthold, 2001; Jones *et al.*, 1996; Salewski and Jones, 2006).

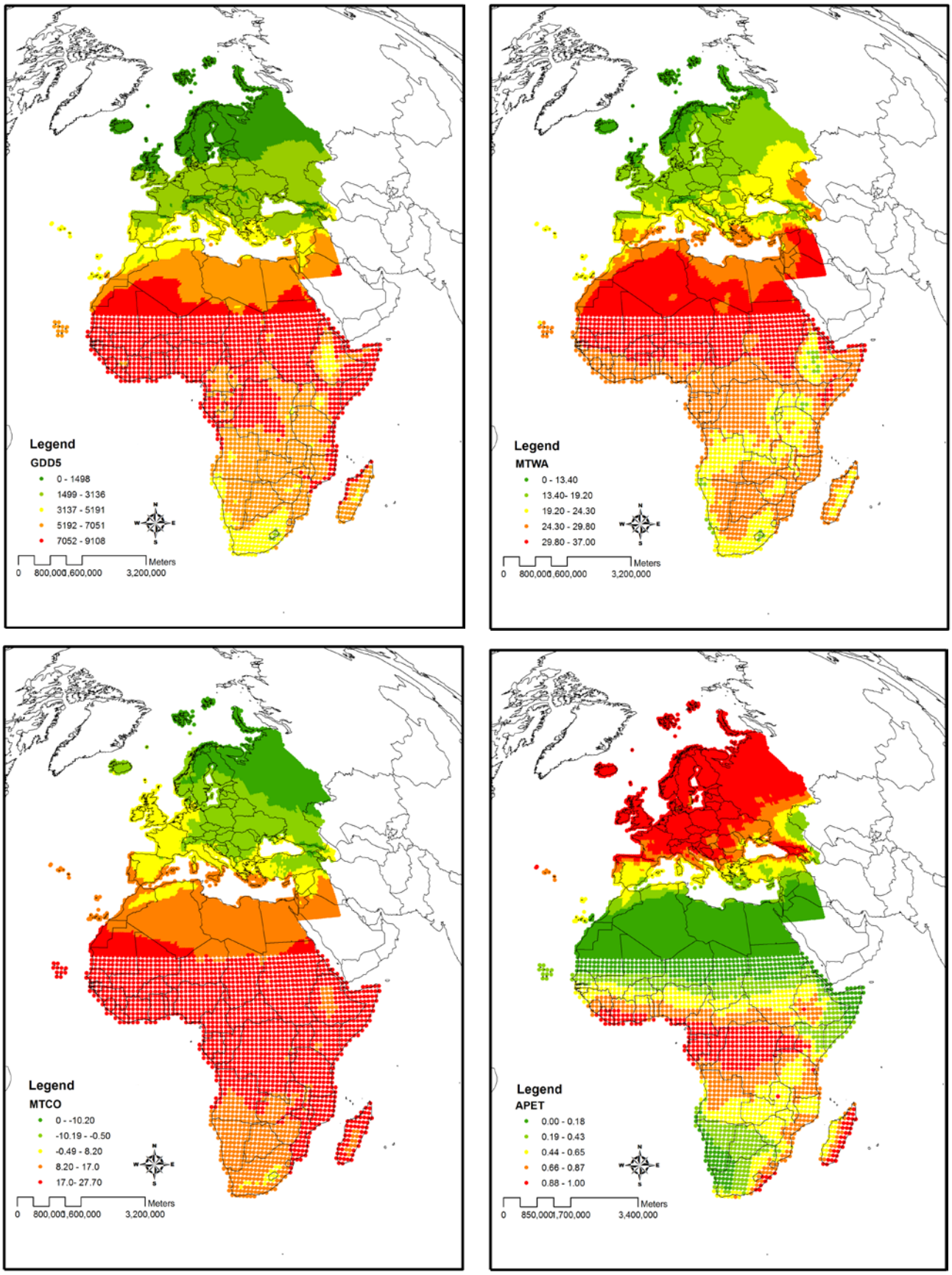


Figure 3.11: Predictor variables that form the base models of the species distribution models: Number of growing days above 5°C (GDD5), Mean temperature of the warmest month (MTWA), Mean temperature of the coldest month (MTCO) and actual to potential evapo-transpiration (APET)

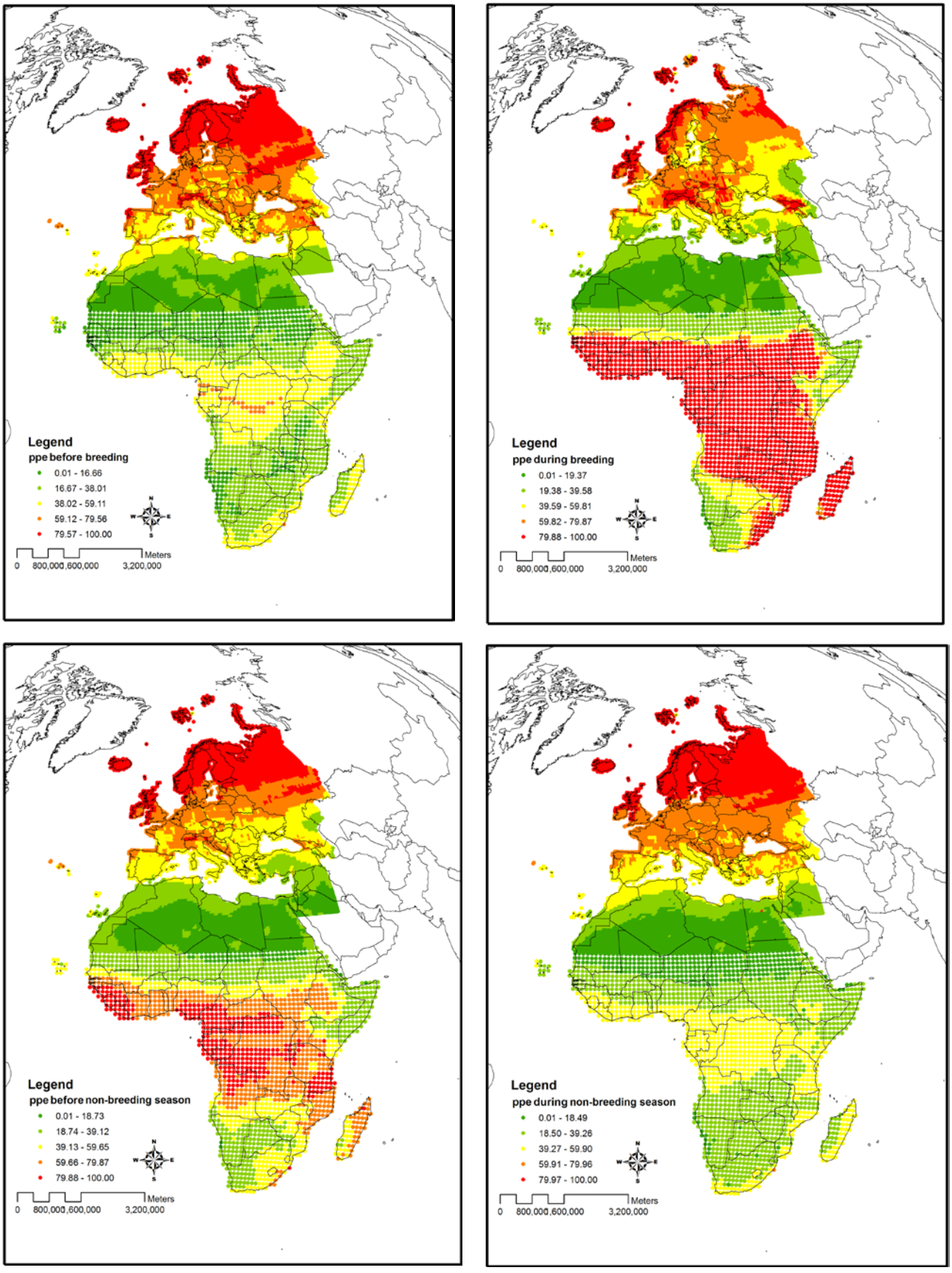


Figure 3.12: Seasonal predictor variables for the study area: difference of precipitation to potential evapo-transpiration (PPE) during the breeding and non-breeding seasons (5 months) and before the breeding and non-breeding season (2 months before). See section 3.1

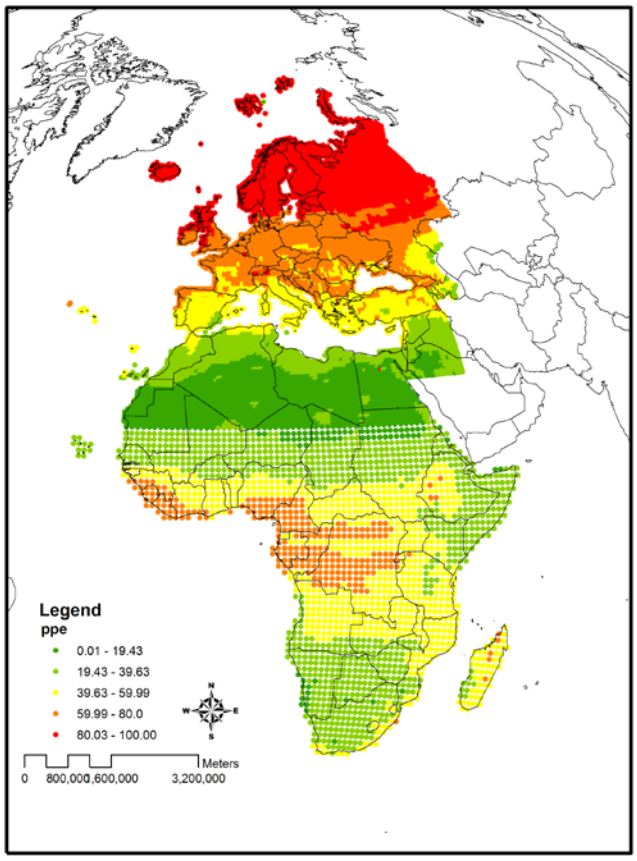


Figure 3.13: Annual Mean PPE (difference of precipitation to potential evapo-transpiration) for the study area

Simulated distributions

Table 3.15 shows that all species have been modelled well, with AUC ranging from 0.798 – 1 for breeding season models and from 0.812 – 0.996 for non-breeding season models (see Section 3.2). Kappa values (see digital appendix) are significantly correlated with AUC (Spearman rho = 0.402 for breeding season models, Spearman rho = 0.512 for non-breeding season models). The maximum kappa was used to set a threshold to convert the probability simulations into presence-absence maps. This was done to enable analyses between present and future simulated maps (see Chapter 4). Converting probability maps into presence-absence, results in a loss of information, which can lead to a poorer quality output (low Kappa values). Differences between AUC and Kappa are due to the fact that AUC measures the discriminatory ability of the models, i.e. how well presences are distinguished from absences, while Kappa measures the overall accuracy of the models' predictions, in terms of commission and omission errors, over the accuracy expected to occur by chance (Allouche *et al.*, 2006). However, many authors have criticised Kappa because it is sensitive to prevalence (Fielding and Bell, 1997; Manel *et al.*, 2001; McPherson *et al.*, 2004) and the definition of

chance is problematic (Vaughan and Ormerod, 2005). Kappa measures the agreement beyond chance (von Eye & von Eye, 2005). The problem with the definition of 'chance' in Kappa is that the specific model of chance chosen can influence the value of Kappa (see Brennan and Prediger, 1981). Allouche *et al.* (2006) recommend using a measure called the True Skill Statistic (TSS) to evaluate models rather than Kappa. However, although in itself it is independent of prevalence, if used as a means to select a threshold it does affect the predicted prevalence of the maps (Freeman and Moisen, 2008). Freeman and Moisen (2008) indicate that maximised Kappa is one of the best measures for selecting thresholds.

As seen in Section 3.2, the overestimations in prevalence are systematic. Many species whose breeding or non-breeding grounds are found in the Mediterranean region have simulated distributions also occurring in South Africa (Fig. 3.14). Some of this over-prediction can be explained by looking at Fig. 3.5 and Figs 3.11-13. Climatically, South Africa is very similar to the Mediterranean region. It therefore makes sense that a model relating climate to species' distributions simulates presence in climatically similar regions.

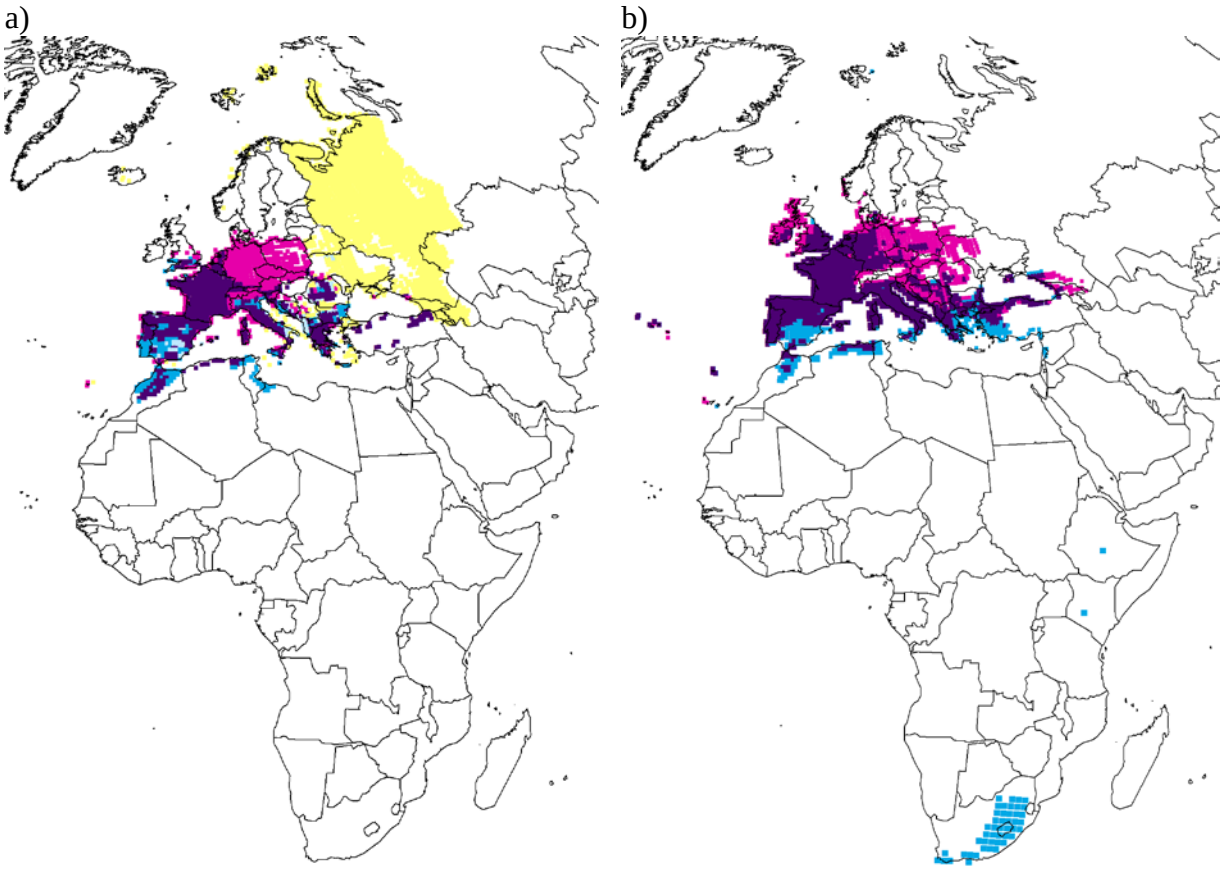


Figure 3.14: Distribution of *Regulus ignicapillus* a) observed and b) simulated. Pink cells indicate breeding, blue non-breeding, purple resident or both breeding and non-breeding. Yellow represents no data values in the EBCC atlas. (Projection is Lambert-Azimuth)

Some species are simulated to occur on islands with similar climate to their present distribution, such as Madagascar, when in fact they are not present (Fig. 3.15). These

discrepancies in the climate-species relationship can also be explained through 1) quality of observed data: 'absences' may not be real absences because failing to detect a species does not necessarily mean that it is absent (Gu and Swihart, 2004; Ottaviani, *et al.*, 2004); 2) factors such as distance and barriers or dispersal (Davis *et al.*, 1998); 3) historical factors (Levin, 1992); 4) biotic interactions/competition, as argued by Hutchinson's realised niche theory (Hutchinson, 1957; Pulliam, 2000). These factors may all contribute to species not being able to occupy all areas that are suitable.

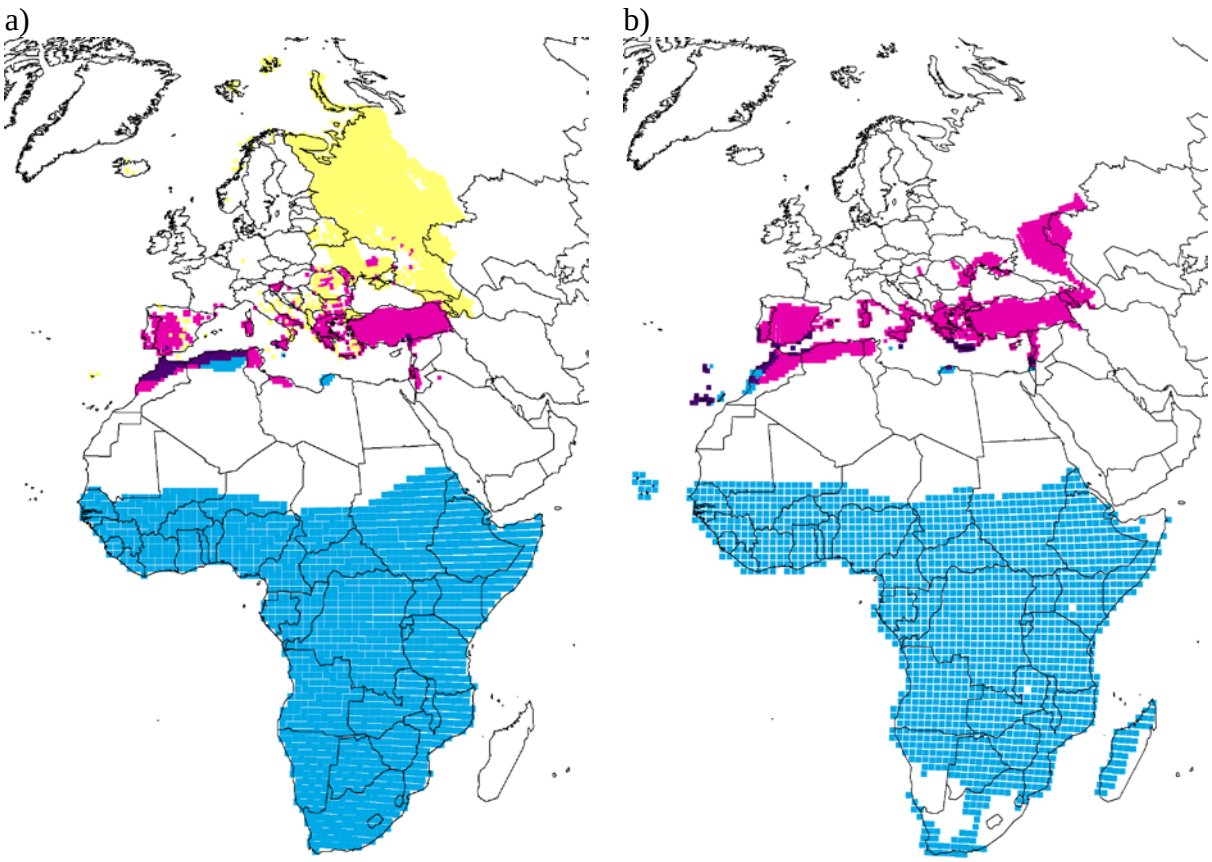


Figure 3.15: Distribution of *Falco naumanni* a) observed and b) simulated. Pink cells indicate breeding, blue non-breeding, purple resident or both breeding and non-breeding. Yellow represents no data values. (Projection is Lambert-Azimuth)

Descrepancies between the observed and simulated maps may also be due to the modelling framework. For example, although many species occur in the Nile region, no simulation reproduces this (Figs. 3.16-17); not even in the CRS models which describe the observed data best (Section 3.2; c.f. digital appendix). Indeed, there is no large-scale distinct climate along this river (Figs. 3.11-13). In these areas, habitat is likely to be key in determining suitability. Since habitat was not included in the models, these areas are not simulated as suitable by the climatic envelope models. In this instance, the scale at which distributions are modelled is

also an issue. Indeed the models also fail to simulate occurrences (Fig. 3.16) in the Sahara desert which probably relate to oases.

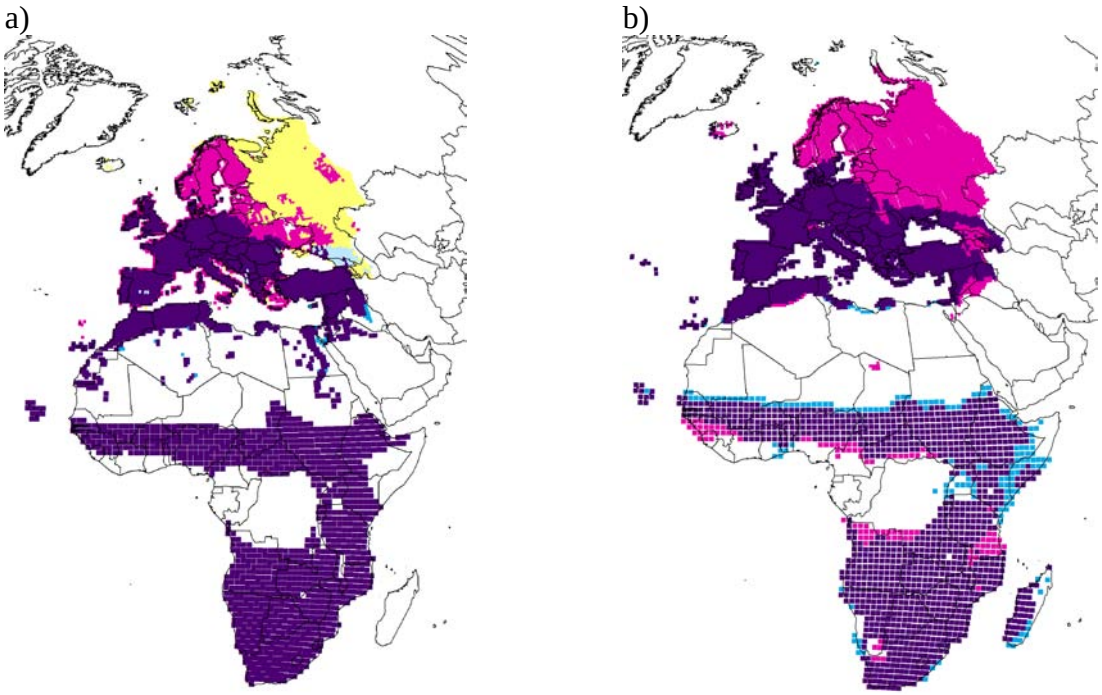


Figure 3.16: Distribution of *Falco tinnunculus* a) observed and b) simulated. Pink cells indicate breeding, blue non-breeding, purple resident or both breeding and non-breeding, yellow represents no data values while the light blue represents wintering in the no data zone.

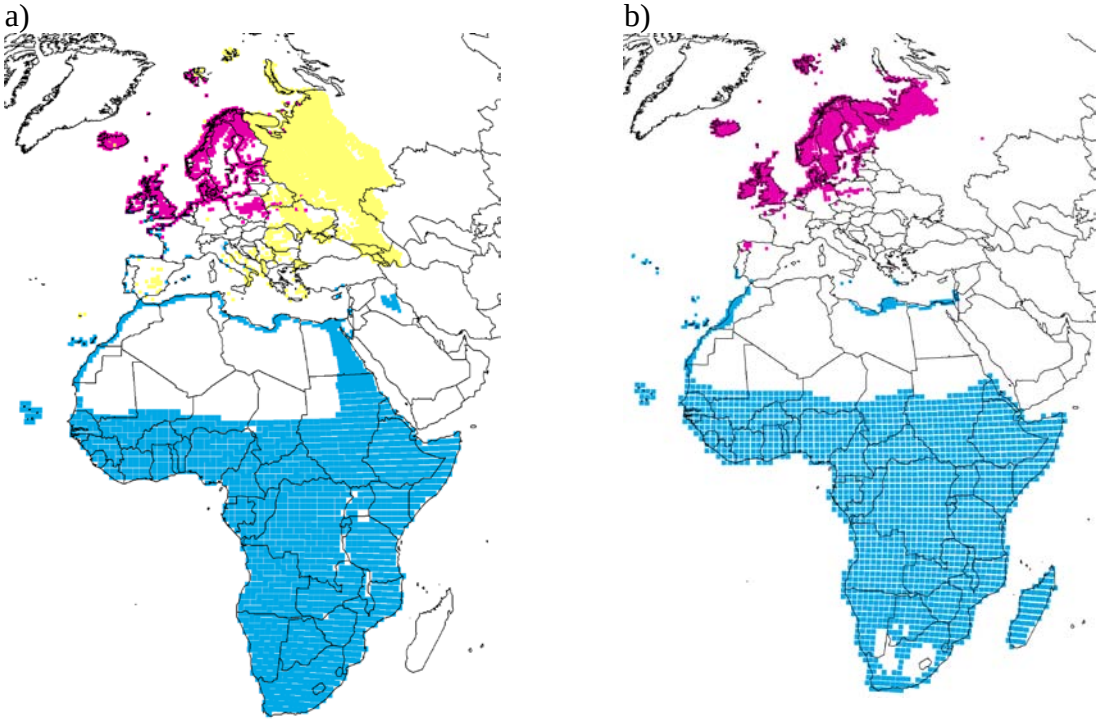


Figure 3.17: Distribution of *Charadrius hiaticula* a) observed and b) simulated. Pink cells indicate breeding, blue non-breeding, purple resident or both breeding and non-breeding, yellow represents no data.

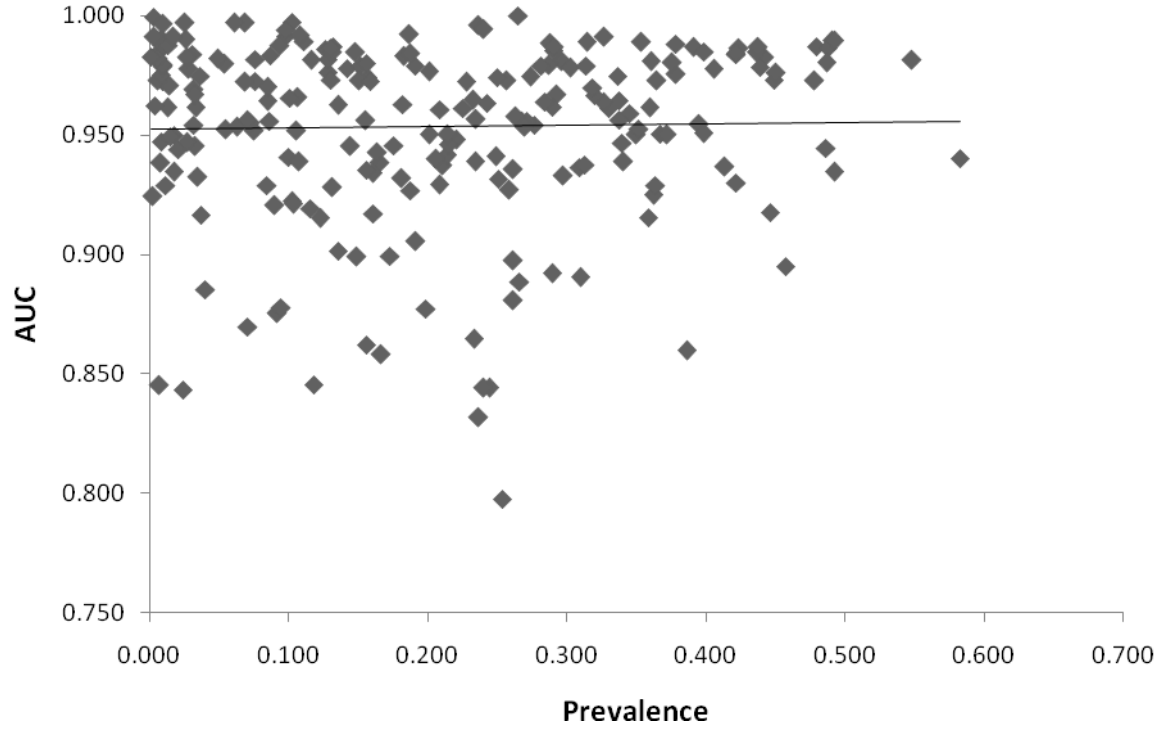
3.3.3 Factors affecting model performance

Other than the errors caused by the model and the modelling method, ecological factors may also determine how well a model performs (Hernandez *et al.*, 2006; McPherson *et al.*, 2004; Segurado and Araújo, 2004). Consequently, I investigated how certain ecological attributes of a species may impact on how well one can model its distribution using climatic variables. These ecological traits were distribution extent (widespread or restricted with a cut off prevalence of 0.3), tolerance, biome, habitat and migration strategy (whether a species is a trans-Saharan migrant or not). To examine whether any of these traits have an effect on model performance (AUC), a factorial ANOVA was done with Tukey's *post hoc* tests. Before this analysis however, AUC was adjusted for prevalence (Eq. 3.10; Huntley *et al.*, 2004; Huntley *et al.*, 2007). Although many studies have found that AUC is not affected by prevalence compared to Kappa (Fielding and Bell, 1997; Manel *et al.* , 2001; McPherson *et al.*, 2004), recent studies have found that AUC may in fact be affected by prevalence (Huntley *et al.*, 2004; Lobo *et al.*, 2007; Maggini *et al.*, 2006).

$$AUC_{adjusted} = a + b * (0.5 - p) \qquad (3.10)$$

Where *a* is the species' AUC, *p* is the species' prevalence and *b* is the regression coefficient from a regression between prevalence and AUC. The regression between prevalence and AUC revealed that prevalence did not affect model performance in the breeding season models ($R^2 = 0.001$, $p = 0.529$; Fig. 3.18 a) but that it did in the non-breeding season models ($R^2 = 0.119$, $p < 0.0001$; Fig. 3.18 b).

a)



b)

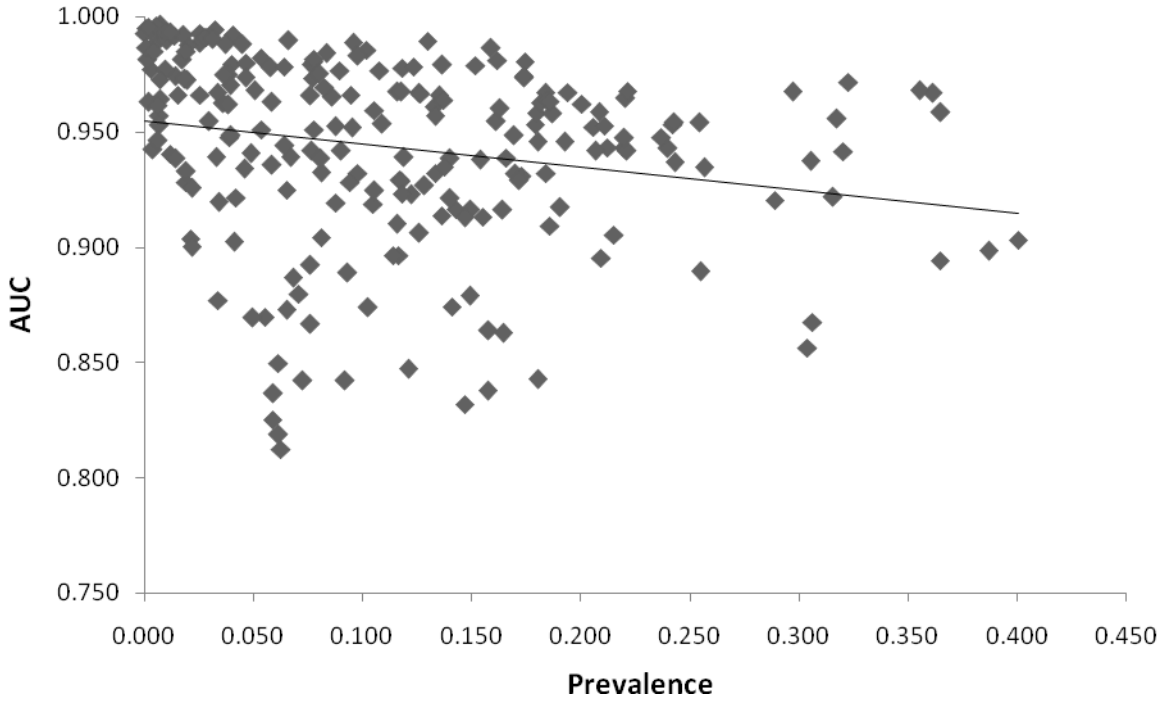


Figure 3.18: Relationship between model performance (AUC) and prevalence with a linear trend line on a) the breeding grounds and b) the non-breeding grounds

The results showed that the performance of models on the breeding grounds is affected by biome ($F_6 = 7.386$, $p < 0.0001$), though effect size was low ($\omega^2 = 0.173$). There was no significant effect of migration strategy ($F_1 = 3.435$, $p = 0.065$), habitat ($F_6 = 1.723$, $p = 0.117$), extent ($F_1 = 0.554$, $p = 0.457$) or tolerance ($F_1 = 1.726$, $p = 0.190$). The *post hoc* tests showed that species whose main biome was tropical grasslands (i.e. those migrants also breeding in Africa) were less well modelled than other species except those breeding in Mediterranean forests or desert. Those species with breeding distributions in Boreal forests were modelled best.

The results showed that the performance of models on the non-breeding grounds were affected by biome ($F_5 = 11.890$, $p < 0.0001$, $\omega^2 = 0.217$), habitat ($F_6 = 6.605$, $p < 0.001$, $\omega^2 = 0.156$), tolerance ($F_1 = 19.548$, $p < 0.0001$, $\omega^2 = 0.084$) and extent ($F_1 = 6.772$, $p < 0.05$, $\omega^2 = 0.031$). Migration strategy did not affect model performance ($F_1 = 2.865$, $p = 0.092$, $\omega^2 = 0.013$). Although models for widespread species and generalist species had significantly lower performance than for restricted and specialist species, the effect sizes were very small. Biomes and habitats to which species belonged to did have an effect on model performance albeit with low effects. The *post-hoc* analyses showed that the distributions of wetlands and coastal species were less well modelled than those of forest or scrub species. The ranges of species whose main biomes were temperate broad leaf and mixed forest, Mediterranean forests or desert were less well modelled that those of other species.

These results corroborate those of other studies examining the effect of prevalence and species' characteristics on distribution models. Prevalence and sample size have been shown to affect the performance of models (Manel *et al.*, 2001; McPherson *et al.*, 2004; Stockwell and Peterson, 2002). The effect of prevalence is largely a statistical phenomenon in that it affects the measures of performance (Fielding and Bell, 1997; McPherson *et al*, 2004). However, a species' marginality seems to be an ecological predictor of how well an SDM will perform. Here I use 'marginality' to mean how distinctive a species' niche is. This is a combination of its major biome and tolerance. Brotons *et al.* (2004), Seguardo and Araújo (2004) and Huntley *et al.* (2007) all found that more marginal species had better performing models. Brotons (2004) suggested two possible reasons why widespread generalist species' models may not perform so well. First, the species may not be limited by the predictor variables used at the scale they are used. Second, different populations of the species may show regional differences in ecological characteristics meaning that, by modelling them together, accuracy is lost. The predictor variables used will also account for how well species' models perform as evidenced by coastal or wetland species' models performing less well: habitat may be more important than climate for these species.

3.3.4 Discussion

The species distribution models generally perform well but show some systematic discrepancies. Discrepancies with the observed data are in part due to the fact that the species have been modelled on a coarse scale relating climate to their distribution. The results indicate that climate is not the sole factor limiting species' distributions. Bioclimatic variables alone were used so that the effect of climate change could be investigated (Chapter 4). There are other errors and uncertainties in the models which, along with the limitations of the modelling approach, will be discussed in the following paragraphs.

Prediction errors are inevitable in SDM (Barry and Elith, 2006; Van Horne, 2002). These errors can be due to theoretical assumptions, data deficiencies and the model framework and specification.

Theoretical assumptions

Species' distribution modelling is underpinned by two main theoretical concepts: niche and equilibrium. SDM rely on the niche concept (Guisan and Zimmermann, 2000) because they assume that species respond to environmental factors. Most modellers state that only a species' realised niche can be modelled (Kearney, 2006; Pulliam, 2000; Soberon, 2007) but there is in fact no evidence that this is truly the case (Guisan and Thuiller, 2005). Nevertheless, the assumption of whether the realised or fundamental niche is the modelled niche has consequences when projecting the resulting models into change scenarios. Indeed, if the realised niche is modelled, the modelled future distribution may not hold if the realised niche changes.

Species distribution models also implicitly assume that there is equilibrium between the environment and species' distributions (Guisan and Zimmermann, 2000). However, data collected represent only a snapshot of reality (Guisan and Thuiller, 2005) and so it is not certain that species are in equilibrium. For instance, many bird species are still expanding their ranges (Newton, 2003). Equilibrium can potentially be estimated with the collection of atlas surveys over time.

Data errors

Uncertainty and errors can be introduced at any stage. Error can be found in the response data or the predictor variables. In species' distribution data, errors can be caused by biases in the

sampling regime, errors in data handling (Graham *et al.*, 2007; Gu and Swihart, 2004; Loiselle *et al.*, 2007), species' detectability and false absences (Barry and Elith, 2006; Gu and Swihart, 2004). Biased data result in the modelled relationships being dominated by patterns at the sampled sites rather than 'real' patterns, which causes spatial error and uncertainty (Barry and Elith 2006). Moreover, false absences may lead either to a false estimation of the species-environment relationship or a pessimistic view of model performance. Classification errors can also occur. For instance, *Anthus trivialis*, *Carduelis carduelis* and *Carduelis chloris* were misclassified in this thesis as forest species. These species in fact inhabit open areas with trees. The effect of these errors is not known. However, the effect is likely to be small given these three species are but 1.3% of the total number. Errors in predictor variables are also possible either due to mismeasurement, transformation (Austin, 2002), or interpolation (Burrough and McDonnell, 1998). Getting data that concord in space, time (Rushton *et al.*, 2004) and scale (Guisan *et al.*, 2007; Guisan *et al.*, 2006) may also lead to errors.

Errors resulting from the data used in this study may be introduced from any of these sources. However, everything has been done to minimise the impact of these errors. For instance the modelling technique used (GAM) has been shown to be robust to errors in distribution data (Graham *et al.*, 2007) and has the flexibility to overcome any oddities in the predictor variables (Austin, 2002).

Model framework and specification

The choice of variables used in the modelling process has a big impact on model uncertainty. Obtaining relevant proximal variables is difficult which is why many distal variables are used in species' distribution modelling (Austin, 2002; Guisan and Zimmermann, 2000). Moreover even if relevant proximal variables are available, our knowledge of species may not be sufficient to know which variables to use (Barry and Elith, 2006) which may lead to a poorer model. Another problem is that we may not have enough data (power) to distinguish meaningful predictors. Missing covariates may not just be due to an imperfect knowledge of factors affecting species' distributions. The aims for a particular model may also cause such limitations. For instance, I found that wetland species' models were poorer and also that the occurrence of many species in the Nile Valley region was not simulated correctly. The inclusion of habitat variables seems necessary to these models (though the scale of the variables could be the issue). However, the aim of this study is to project the models into the future. While we have good models of future climates, we do not have good models of future land cover. Therefore, this limitation has to be accepted. It was hoped, when this study was

started, that modelling at a coarse scale would mitigate the effects of not including land cover. Indeed, Thuiller *et al.* (2004) found that land cover variables in bioclimatic models did not improve predictive performance. They hypothesised that this may be either because climate explains land cover or that the models were at a coarse resolution (50 km x 50 km) which meant that the heterogeneity of the landscape was lost. On a finer grid, however, land cover variables become very important (Hill *et al.*, 2002).

Model specification errors are very common because the "truth" is not known. Barry and Elith (2006) suggest that these errors will mainly occur if the "true" model is not contained in the model specification, for instance if the true relationship is quadratic but a linear model is specified. If the "truth" is contained in the model specification and if there is a large enough sample size, then the model estimated will converge towards the "truth" (at least when using maximum likelihood techniques; Barry and Elith, 2006; Welsh, 1996).

How techniques estimate the shape of response surface can also cause uncertainties. Some relationships may be linear but others may be more complex (Austin 2002). The relative success of flexible techniques compared with more strict techniques, such as logistic regression or GLM, in this study shows that species-environment relationships are complex. However, overfitting can be an issue when modelling complex relationships. Although this study has tried to select the most robust model, without being able to ascertain the validity of the models under a variety of independent trials, overfitting may be a problem. Moreover, each modelling technique will have its own biases and assumptions making it difficult to quantify the uncertainty in the models (Burgman *et al.*, 2005).

Finally, error in the modelling framework will lead to discrepancies that originate from statistical or seemingly ecological artefacts. For instance all niche models are sensitive to sample size and bias in the distribution of data (Araújo and Guisan, 2006). Many niche models are affected by species' ecological traits (see section 3.3.3). However, this is more of a model specification problem: covariates are missing from the model.

3.3.5 Conclusion

Uncertainty in SDM originates from many sources. It is impossible to eliminate uncertainty from models because of the fact that they are models. Moreover, other factors than climate affect species' distributions. This Chapter has shown that good models can be obtained but that the models used carry assumptions and limitations. The author would therefore urge the reader to keep in mind these limitations and caveats in reference to the results presented in this study.

4. Projecting species' ranges into future climate change scenarios

Global temperature has increased by about 0.76° C over the last 100 years (Solomon *et al.*, 2007). Species have responded to this change by shifting their ranges polewards (Walther *et al.*, 2002; Parmesan and Yohe, 2003) or by shifting elevation ranges upwards (Shoo *et al.*, 2005; Wilson *et al.*, 2005). Projected future climate change of between 1.1-6.4° C over the next 100 years (Solomon *et al.*, 2007) may therefore have a profound effect on species' ranges.

Climate change projections are achieved using General Circulation Models (GCM) and emissions scenarios (see Chapter 2). The Fourth Assessment Report of the IPCC (AR4) gives a detailed account of the workings and evaluation of these GCM. Although each climate model produces different simulations, when combined (termed multi-model mean) they closely simulate the current observed climate (Solomon *et al.*, 2007). In this chapter three GCMs (Echam5 [Jungclaus *et al.*, 2006], GFDL-CM2.1 [Delaworth *et al.*, 2006] and HadGEM1 [Johns *et al.*, 2006] will be used, along with two emissions scenarios (A1B and A2; Nakicenovic *et al.*, 2000). These two scenarios represent mid and high range emissions and were selected mainly because of the availability of data sets[1]. Moreover, the great increase in CO_2 emissions in the last decade, suggests that more 'extreme' scenarios may be more appropriate than 'conservative' scenarios (such as B1 and B2) for future climate change projections (Beaumont *et al.*, 2008). Depiction of the anomalies between future and present climate for my study area can be found in the digital appendix. In terms of temperature, Echam is warmer in the Sahel and the Mediterranean than the multi-model mean, GFDL is cooler in West Africa, and HadGEM has higher temperatures in Europe and lower temperatures in Africa. In terms of precipitation, Echam is a 'dry' model, GFDL a 'wet' model and HadGEM matches the mutli-model mean quite closely (Solomon *et al.*, 2007). In terms of the forecast change in climate (compared with the multi-model mean), Echam exhibits a lower change, GFDL a higher change and HadGEM a midrange change compared with all GCM (Solomon *et al.*, 2007).

These differences cover only part of the uncertainty that exists in GCM. Beaumont *et al.* (2007) analysed the internal variability of climate models which arises from slightly different but equally valid initialisations of a climate simulation (each new simulation termed "realisation"). They found that although realisations from a single model were similar to each other, they differed when projected into the future, contributing further to the uncertainty in

[1] Other data sets were not available at the time.

simulations of future climate change. To take this uncertainty into account, multiple realisations of each GCM should be used, but this is currently unrealistic as these are not yet available for many GCM. Uncertainty in projections is a big issue which is why most studies reporting the likely effects of climate change provide a range of values resulting from different GCM and/or scenarios.

Uncertainty is further introduced with the use of species distribution models (SDM). The analyses in the previous chapter indicated that either GAM or CRS were good choices. However, many studies have reported that different modelling techniques produce different future projections (Thuiller, 2004; Araújo *et al.*, 2005b; Dormann *et al.*, 2008). The discrepancies between projections from different SDM result from the different variables in each model or from the different assumptions and forms of each modelling technique. In the previous chapter, I showed that Generalised Additive Models (GAM) and Climate Response Surfaces (CRS) were very similar in their assumptions and produced very similar simulations. In the first part of this chapter, I investigate the potential uncertainty in future projected ranges of migrant birds arising from using different SDM.

In the second part of the chapter, the potential effects of climatic change on European breeding migrant birds are reported. Many studies have reported the potential impacts of climatic change on birds (Huntley *et al.*, 2006; Jetz *et al.*, 2007; Huntley *et al.*, 2008; Jensen *et al.*, 2008), which are similar to the projected impacts on many other species. However, the potential effects on migrant birds are likely to be more complex because these species live in biogeographically distinct areas at different times of the year.

In the third part of this chapter, differences between migrant birds will be investigated. It is possible that certain groups respond differently to climatic change. For instance, many studies have already shown that species with smaller ranges may be more affected by climatic change than widespread species (Doswald *et al.*, 2009; Schwartz *et al.*, 2006; Huntley *et al.*, 2008; Sekercioglu *et al.*, 2008) as small range species often occupy climatically rare space (Öhlemüller *et al.*, 2008). Moreover, some species may be more able to adapt to climatic change (Jonzén *et al.*, 2006). Berthold (2001) hypothesised that long-distance migrants might be more affected than short-distance/resident species. In this section, I investigate these possibilities by testing differences between different migratory groups.

4.1 Comparisons between models on future climate change projections

4.1.1 Introduction

Different modelling methods produce simulated distributions, which are often widely different (in terms of magnitude and direction) when projected onto new data, i.e. data not used during model building, (Thuiller, 2003; Thuiller, 2004; Araújo *et al.*, 2005b). This finding has led many authors to advise a multi-model ensemble or a consensus approach, where a suit of models is used to determine either a range of expected outcomes or a mean/consensus of outcomes (Thuiller, 2004; Araújo and New, 2006; Araújo *et al.*, 2005b; Pearson *et al.*, 2006). Multi-model ensemble approaches use a range of different methods to model species' distributions. The results from multi-model ensembles are presented as a range of values from the different models, as the mean from all the models, or the results from the best model are presented (Thuiller, 2004; Araújo and New, 2006). In consensus modelling, a range of methods is used and the similarities and differences between the methods are analysed. Those models that are the most similar (as well as proving to be most accurate) are then used (Araújo and New, 2006). Araújo *et al.* (2005b) investigated the use of consensus forecasting. They modelled the breeding ranges of 116 birds and projected these into future climate change scenarios. They used four different modelling techniques, two data parameterisations and two rules to transform probabilities of occurrence into presence-absence models resulting in 16 possible different models. They found that consensus models (those that differed least from the mean forecast) performed best using AUC and Kappa as the performance metrics. Moreover, using the average of the consensus models performed even better than using the mean of all models (Araújo *et al.*, 2005b). Pearson *et al.* (2006) argued that differences in projections can be mainly accounted for by the types of data they required and the assumptions each made. Indeed they found that techniques could be grouped by these characteristics and that those in the same group produced similar projections. All the methods used in Araújo *et al.* (2005b), on the other hand, have different assumptions which may explain some of the differences when they are extrapolated onto new data.

Here I further investigate this issue with three modelling methods to project the species' distributions into a potential future climate, in order compare how different models project. It is expected that GAM and CRS will produce similar projections (since they have similar assumptions) whilst GLM will be the most different.

4.1.2 Methods

Climate data

Precipitation, temperature and cloudiness anomalies were taken from the GFDL Atmosphere-Ocean General Circulation model (Delaworth *et al.,* 2006), scenario A1B (Nakicenovic *et al.,* 2000), for the 2085 time-slice, i.e. mean of 2071-2100. The anomalies (relative to the climatic norm of 1961-1990) were fitted to a longitude x latitude grid using a spline surface (method describe in Hutchinson, 1989) and then were interpolated to the study area using the spline surfaces (using algorithm in Numerical Recipes Software, 1988-1992). These variables, in conjunction with soil texture, were transformed to provide the set of bioclimatic variables used in Chapter 3.

Models and analyses

The species distribution models discussed in Chapter 3 were fitted to the recent climate (1961-1990) and then projected onto the new 'future' bioclimatic variables. The probability of occurrence for each model were correlated (Pearson's correlation) so that a correlation matrix similar to that in Chapter 3 could be obtained. The probability values were then transformed into presence-absence (p-a) or binomial values using the maximised kappa threshold obtained from the present day models. These values were correlated (Spearman correlation) to investigate similarities between modelling method.

The future p-a grids were compared with the present-day p-a grids. Percentage overlap (O) was calculated as the proportion of grid cells classified as present in both the current and future simulations. Before this was done, the one degree grid cells of the non-breeding range were multiplied by four so as to be equivalent to the half degree breeding range. Relative change of range extent (R) was calculated by dividing the future range extent (number of cells indicated projected as occupied in the future) by the present-day range extent (number of cells occupied in the present-day). The centroid of each seasonal distribution range was calculated as the mean longitude/latitude. The geodesic distance (D) between the present day centroid and the future centroid was calculated using a "Geodesic" program written in Fortran by B. Huntley which used the solution of Sodano and Robinson (1963). This program also calculated the first and last azimuth. The first azimuth (θ) gives us the angle of shift of the distribution range. The Geodesic program was also used to calculate the average 'migration distance' (M) by incorporating the centroids of each seasonal range. 'Migration distance' is here defined as the geodesic distance between the breeding and non-breeding range centres,

measured in Kms by a straight line (Doswald *et al.* 2009 – see Appendix I). Species richness (N) per grid square was calculated for both the present day and future simulations.

Repeated measures ANOVA[2] were performed to analyse the effect of the different modelling methods on proportion overlap (O) and relative change extent (R). Proportion overlap was arcsine square-root transformed, while the relative change of extent was logged to normalise the data. Friedman repeated measures tests (Field, 2005) were performed to examine the effect of modelling method on the shift in range between present and future and migration distance for both the current models and the future models. The Watson-Williamson test (Zar, 1996) was used to examine whether the mean angle of shift was different between modelling methods. Relative change in species richness was calculated and differences between models were examined using Friedman's repeated measures tests.

As well as these comparisons between present and future models for each method, future maps were also compared between the modelling methods. This was done by collecting overlap and relative change in extent between predictions. To assess the difference between the future probability maps, the mean absolute error (MAE; Eq. 3.7) for each species between each modelling method was taken. A repeated measures ANOVA was performed to assess whether MAE differed. MAE was arcsine square root transformed before the analyses to normalise the data. To assess the difference between the p-a maps Jaccard's distance index (Jaccard 1901; Eq. 4.1) was calculated for each species.

$$J = \frac{(a+b)}{(a+b+c)} \tag{4.1}$$

Where *a* is all presences for model 1 but not model 2, *b* is all presences for model 2 but not model 1 and c is all presences in both model 1 and model 2.

This equation measures the difference between models and values close to 0 mean that the output is very similar and close to 1 that they are very different. Repeated measures ANOVA was performed to assess whether Jaccard's index differed between methods. The index was arcsine square root transformed before the analyses to normalise the data.

[2] As stated in Chapter 3, page 75, the assumption of sphericity needs to be tested. The results of these tests for each ANOVA are reported in Appendix II.

4.1.3 Results

Differences between models on present- future measures

Breeding Range

Figure 4.1 shows the relative change in species richness between the present and future simulations for each model. This shows that on the breeding range, GAM and CRS simulated, on average, reduced species richness in the future but GLM simulates increased species richness. All simulations of species richness change were different (χ^2= 207.14, $p < 0.0001$).

The model used affected species' range overlap (O) between present and future distributions ($F_{(1.84,420.70)} = 250.79$, $p < 0.001$, $\omega^2 = 0.524$). Bonferroni *post hoc* tests showed all methods were significantly different from each other ($p < 0.001$) in terms of overlap.

The models did not differ in their simulations of change in range extent ($F_{(1.53,349.14)} = 1.878$, $p = 0.164$, $\omega^2 = 0.008$).

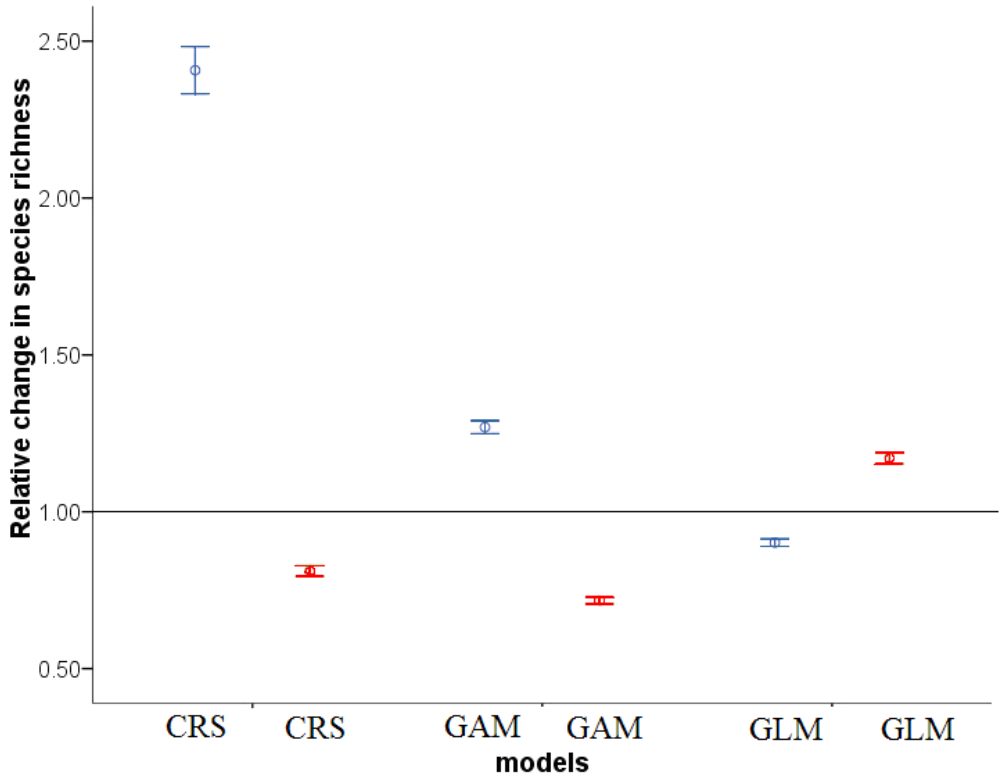


Figure 4.1: Mean and confidence interval range for the relative change in species richness between 2085 GFDL AOGCM - scenario A1B simulations and present day simulations for each modelling method. Blue represents non-breeding season models and red the breeding season models. Horizontal line represents no change between present and future range size.

Shift in median centres were significantly different between modelling techniques (χ_2 = 54.93, $p < 0.0001$). CRS predicted a greater shift than either GAM or GLM. Although all methods simulated a north-easterly shift in range (CRS: 11.70º, GAM: 21.27º, GLM: 29.03º), the mean direction of shift was statistically different between models ($F_2 = 7.34$ $p < 0.05$).

Non-breeding Range

All models simulated different changes in species richness between present and future periods for the non-breeding range ($\chi^2 = 3532.09$, $p < 0.0001$). Both CRS and GAM simulated a mean increase in species richness (Fig. 4.1), although CRS more so than GAM. GLM simulated a decrease in species richness.

The model type had an effect on overlap ($F_{(1.90,434.16)} = 264.222$, $p < 0.001$, $\omega^2 = 0.537$). Bonferroni *post hoc* tests showed that O for all the methods were significantly different from each other ($p < 0.001$).

The modelling technique used also affected species' range extent ($F_{(1.32,87.36)} = 6.291$, $p < 0.01$, $\omega^2 = 0.027$). Bonferroni *post hoc* tests showed that the change in range was significantly different between GAM and CRS ($p < 0.03$) and GLM and CRS ($p < 0.02$) but not between GAM and GLM.

The modelled shift in centroids was different between models ($\chi^2 = 125.52$, $p < 0.0001$). CRS predicted a greater shift than either GAM or GLM. Mean direction of shift in range was north easterly (CRS: 20.18º, GAM: 39.26º, GLM: 17.05º) but was significantly different between models ($F_2 = 4.57$ $p < 0.05$).

Migration Distance

The Friedman tests analysing the effect of modelling method on migration distance revealed that there was a significant effect of method for both the present-day migration distance ($\chi^2 = 139.07$, $p < 0.0001$) and the potential future migration distance ($\chi^2 = 25.52$, $p < 0.0001$).

Future-future differences

The correlations coefficients and the standard deviations for the future probability output for the models are shown in Tables 4.1-2 and Tables 4.5-6 while the correlation coefficients and standard deviations for the p-a output are shown in Tables 4.3-4 and Tables 4.7-8. These show

that GAM and CRS had higher mean correlation coefficients and smaller standard deviation than the other model combinations.

Table 4.1: Mean Pearson correlation coefficients for the breeding range models

Models	GAM	GLM	CRS
GAM	1.000		
GLM	0.696	1.000	
CRS	0.851	0.603	1.000

Table 4.2: Standard deviations for the breeding range Pearson correlations

Models	GAM	GLM	CRS
GAM	1.000		
GLM	0.275	1.000	
CRS	0.105	0.276	1.000

Table 4.3: Mean Spearman correlation coefficients for the breeding range models

Models	GAM	GLM	CRS
GAM	1.000		
GLM	0.561	1.000	
CRS	0.646	0.488	1.000

Table 4.4: Standard deviation for the breeding range Spearman correlation

Models	GAM	GLM	CRS
GAM	1.000		
GLM	0.266	1.000	
CRS	0.221	0.247	1.000

Table 4.5: Mean Pearson correlation coefficients for the non-breeding range

Models	GAM	GLM	CRS
GAM	1.000		
GLM	0.738	1.000	
CRS	0.817	0.584	1.000

Table 4.6: Standard deviations for the non-breeding range Pearson correlations

Models	GAM	GLM	CRS
GAM	1.000		
GLM	0.196	1.000	
CRS	0.116	0.212	1.000

Table 4.7: Mean Spearman correlation coefficients for the non-breeding range

Models	GAM	GLM	CRS
GAM	1.000		
GLM	0.471	1.000	
CRS	0.534	0.371	1.000

Table 4.8: Standard deviation for the non-breeding range Spearman correlation

Models	GAM	GLM	CRS
GAM	1.000		
GLM	0.267	1.000	
CRS	0.219	0.254	1.000

The differences between probabilities of occurrence from each model were smaller between GAM and GLM for the non-breeding models and between the GAM and CRS for the breeding models (Fig.4.2). However, MAE was significantly different between models on both the breeding ($F_{(1.48,337.42)} = 207.16$, $p < 0.0001$, $\omega^2 = 0.476$) and non-breeding grounds ($F_{(1.48,338.80)} = 185.45$, $p < 0.0001$, $\omega^2 = 0.449$).

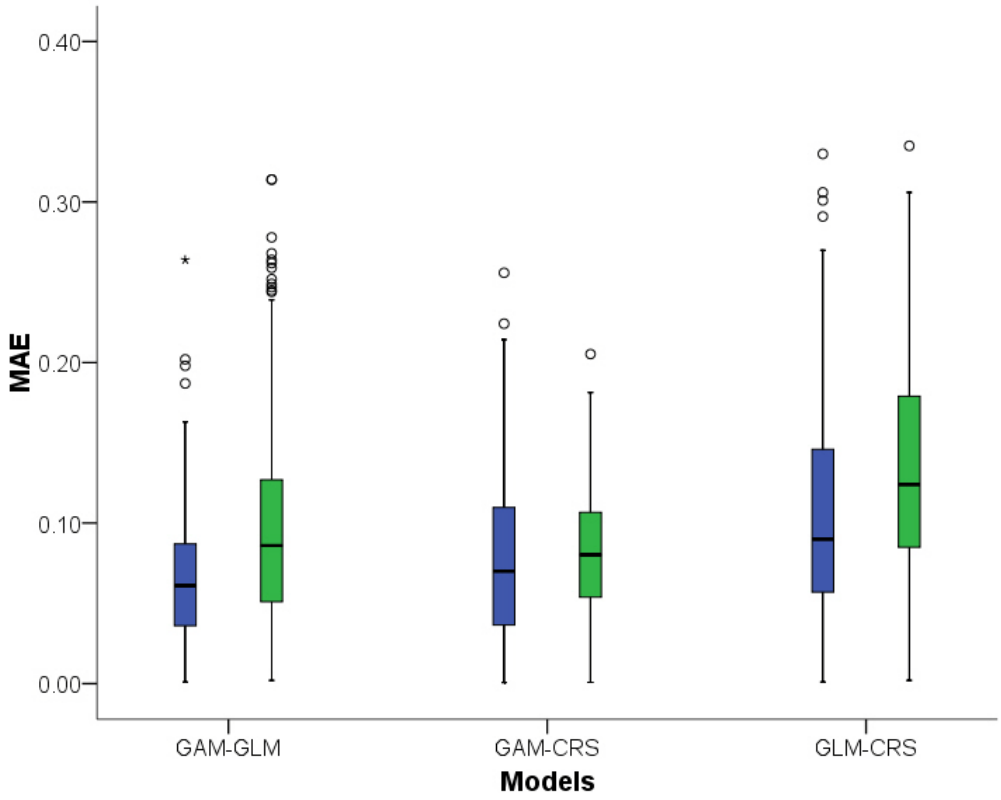


Figure 4.2: Mean Absolute Error (MAE) between probabilities of occurrence between the different models. Blue represent the non-breeding season models while the green represents the breeding season models

If the future simulations produced by each method were the same, one would expect a high percentage overlap between the different future simulations. However, as shown in section 3.2.3 prevalence differed between each modelling method. Therefore, overlap will not be very high nor will range change be close to null, as different methods will predict more or less prevalence. The mean, standard deviation and median overlap and range change between each method is shown in Table 4.9. Overlap is highest between CRS and GAM showing that the future projections from both methods are similar. Range extent is lowest between GLM and GAM meaning these methods project similar magnitude of range change.

Table 4.9: Mean, standard deviation and median values for breeding and non-breeding overlap and range change between future simulations from GAM, GLM and CRS

Models	Season	Statistic	Mean	Standard deviation	Median
CRS_GAM	Breeding	**Overlap**	**0.581**	**0.246**	**0.637**
		Range Change	1.320	1.756	0.978
	Non-breeding	**Overlap**	**0.457**	**0.243**	**0.444**
		Range Change	1.489	1.685	1.083
CRS_GLM	Breeding	**Overlap**	**0.448**	**0.250**	**0.437**
		Range Change	0.826	0.616	0.765
	Non-breeding	**Overlap**	**0.331**	**0.261**	**0.251**
		Range Change	1.194	1.319	0.814
GLM_GAM	Breeding	**Overlap**	**0.512**	**0.271**	**0.532**
		Range Change	0.859	0.899	0.766
	Non-breeding	**Overlap**	**0.391**	**0.275**	**0.343**
		Range Change	0.962	0.905	0.828

The difference between the p-a grids produced by each method was significantly different between models on both the breeding ($F_{(1.64,374.09)} = 92.56$, $p < 0.0001$, $\omega^2 = 0.289$) and non-breeding grounds ($F_{(1.72,393.70)} = 73.35$, $p < 0.0001$, $\omega^2 = 0.243$). However, GAM and CRS have the smallest differences (Fig. 4.3).

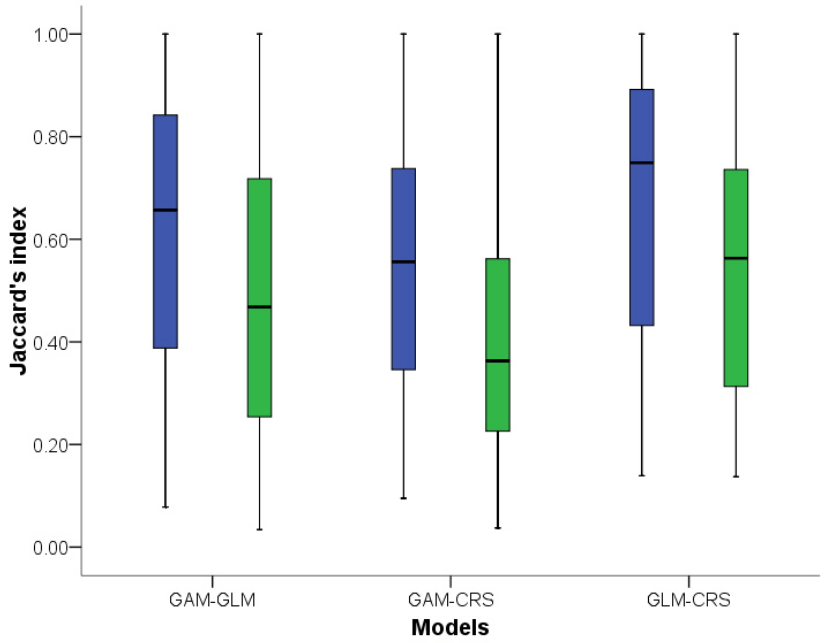


Figure 4.3: Jaccard's index for the differences between models. Values close to 0 indicate less difference and 1 more difference. Blue represents the non-breeding season models and green the breeding season models

4.1.4 Discussion

The results show that the future projections from each method were different from one another in magnitude of change but not necessarily in direction of change. Percentage overlap was significantly different for all modelling techniques, as were shift in centroids and migration distances. Mean angles of shift were also different among models though were all in a northerly direction. Changes in range extent values were different on the non-breeding range, except between GAM and GLM; but were similar on the breeding range. Change in future species richness showed that both CRS and GAM simulated reduced species richness on the breeding grounds and an increase on the non-breeding grounds whilst GLM simulated the opposite (Fig 4.1). These differences in results between methods are in part due to the fact that, as demonstrated in the last chapter, projected species' prevalences are different between methods. Indeed there is a consistent scale of predicted prevalence, with CRS simulating the least number of presences and GLM the most for a given species. The values calculated (e.g. Overlap, Relative range extent, Direction of shift, Number of species per grid cell) are therefore different among modelling techniques.

Comparisons of each method's future simulated output were more revealing, despite the influence of prevalence on the results. Correlation analyses on both the probability of occurrence output and the presence-absence output show that GAM and CRS were most similar, with higher mean correlation coefficients and lower standard deviations. The mean correlation coefficients were higher for the raw probability values than for the presence-absence maps. This raises the question, how much does the imposition of a threshold change a model's output? Araújo *et al.* (2005b) found that different rules to transform probabilities into presence absence had an effect on variability of the models. Both Lui *et al.* (2005) and Jiménez-Valverde *et al.* (2007) argued that there has not been enough testing of different rules to select thresholds. Both studies analysed different threshold criteria on species' distribution. Lui *et al.* (2005) compared ten different threshold-determining approaches on two SDM, while Jiménez-Valverde *et al.* (2007) compared four threshold-determining approaches on virtual species with differing prevalence data. Assessment of model performance used Kappa, sensitivity and specificity. Both studies found that maximised Kappa was deficient as a threshold criterion in some instances, while the use of prevalence or more sophisticated methods, which correlated with prevalence, were generally best. Whilst these studies are exciting in terms of new possibilities, they do not give a clear indication that maximised kappa is not good as a threshold decision criterion. Indeed, the number of species, modelling and assessments of model performance were limited in both studies. Furthermore, a study by

Freeman and Moisen (2008) showed that techniques that maximise kappa were as good as thresholds chosen so that predicted prevalence equalled observed prevalence. Moreover, using prevalence as a threshold (i.e. using a species' prevalence value as a cut off point) produced present-day maps of species' distribution which were more different to the observed data than when using maximised kappa (Figure A1[3]) and, of course, had lower Kappa values. More research is still needed, especially in terms of the use of thresholds in forecasting. Differences seen between models could be due to imposing the present day threshold on a future model.

Both Mean Absolute Error (between future probability maps) and Jaccard's index (based on presence-absence maps) showed that CRS and GAM have the least differences between them. However, all models produced statistically different outputs. Superimposing the future presence-absence maps showed again that GAM and CRS were the most similar as they overlapped most on both the breeding and non-breeding grounds.

The differences in projection found between modelling techniques will be influenced by the differences in simulated current prevalence and will be due in part to the differences in how each technique projects onto novel climates (Williams *et al.*, 2007). Williams *et al.* (2007) showed that new climatic combinations are likely to arise, especially in the tropics and subtropics. Novel climatic conditions will have an unknown effect on species and will also provide incomplete information for models. How each modelling method deals with these no-analogue climates will result in differences among model projections and in prediction errors (Saetersdal *et al.*, 1998; Williams and Jackson, 2007). The CRS modelling method allows the user to investigate where the model extrapolates. Figure A2 shows that CRS extrapolates in Eastern Europe, some areas in the Mediterranean, the Sahara desert and the tropics and sub-tropics. These findings corroborate other studies investigating the distribution of potential novel climates (e.g. Williams *et al.*, 2007).

To demonstrate differences between SDM methods, Elith and Graham (2009) investigated, with the use of artificial species, how five commonly used techniques extrapolate. Their paper rightly argues that modellers need to start analysing how their models work and ask whether the algorithms chosen extrapolate in a manner that makes ecological sense. It is true that, in all studies using SDM, none have properly investigated how their models work and therefore why they differ, only being concerned with which model performs best. Although the investigations into model performance undertaken in this thesis do not investigate these issues as thoroughly as Elith and Graham (2009), they have investigated the conceptual and operational validity of the methods (see Chapter 3), and have tested the hypothesis that how a model extrapolates is due to its assumptions and how it relates species'

[3] Figures and Tables labelled A are in Appendix II

response to climatic variables. Therefore, the investigations undertaken in this thesis are more thorough than some studies, but could have been more complete.

4.1.5 Conclusion

It was hypothesised that both GAM and CRS would have similar projections, leading to the choice of either as the best model (see Chapter 3). However, the variability among the future projections makes this decision difficult. Both techniques were more similar in their projections than GLM. A comprehensive review on climate-envelope models concluded that the "best model performance has been most often attributed to techniques using complex approaches to model fitting" (Heikkinen *et al.*, 2006). Indeed, I found that GAM and CRS both outperformed GLM in both current day predictions (see Chapter 3) and in future predictions in terms of direction of change (e.g. species richness).

Instead of using the best model approach from a multi-model ensemble (Thuiller, 2003; Thuiller, 2004), a consensus framework (Araújo *et al.*, 2005b; Araújo and New, 2006) will be used. However, as Araújo *et al.* (2005b) suggest, only the best consensus models (GAM and CRS), in terms of overall prediction and robustness, will be used in the next sections of this chapter.

4.2 Potential impact of climate change on European breeding migrant birds

4.2.1 Introduction

Many studies have documented the effect of recent climatic change on birds (see Chapter 2). Birds have already responded to the global surface temperature rise (IPCC, 2007) by shifting their ranges and colonising new areas (Thomas and Lennon, 1999; Böhning-Gaese and Lemoine, 2004) as well as adapting to the new climatic conditions (Bearhop *et al.*, 2005; Jonzén *et al.*, 2006).

Projected future temperature rises and precipitation changes are more than likely to continue to affect species. Currently, knowledge of how the majority of species might respond to these changes can only be achieved through predictive modelling. Many studies have already assessed the potential impact of future climatic change on certain species or groups of species (see Chapter 2). These studies all show similar projections: a shift of distributions northwards (mainly North-east) in Europe (Huntley *et al.*, 1995; Araújo *et al.*, 2004; Huntley *et al.*, 2007; Huntley *et al.*, 2008) and an eastwards shift in South Africa (Erasmus *et al.*, 2002; Simmons *et al.*, 2004). Projected changes in Africa are more complex than those for Europe (McClean *et al.*, 2005; Huntley *et al.*, 2006) due to more complex climatic patterns originating from large scale ocean-atmosphere circulations such as the El Niño/Southern Oscillation or the African Easterly Jet (Hulme *et al.*, 2001; Nicholson, 2001).

Huntley *et al.* (2008) projected that European breeding birds' potential future (2085) ranges would decrease between 11% and 28% and overlap by an average of only 31-53% with their current ranges. Ranges would shift northwards (northwest to northeast) on average. Jetz *et al.* (2007) forecast that, by 2100, over 900 birds would face over 50% range reductions from a combination of climatic change and land-use change. To date, all studies of the potential consequences of climatic change on birds' distributions have focused on their breeding ranges. These studies do not show the full impact of climatic change on migratory birds. In this study, I examine the potential consequences of climatic change on migratory birds by modelling future climatic change scenarios on both the breeding and non-breeding ranges of European migrant birds.

4.2.2 Methods

Climate data

Precipitation, temperature and cloudiness variables representing the climate anomalies between the 1961-1990 climatic norm and the future climates were derived from three Atmosphere-Ocean General Circulation models (Echam, HadGEM and GFDL) and two scenarios, A1B and A2, (Nakicenovic *et al.*, 2000), and taken from three 30 year means centred on 2025, 2055 and 2085. The anomalies were added to the climatic norm (see section 4.1.2) and were transformed into several bioclimatic variables as described in Chapter 3 for all 18 permutations.

Models and analyses

The consensus species distribution models, GAM and CRS (see section 4.1), were fitted to the current climate and then projected onto the new 'future' bioclimatic variables. For each time period and emission scenario, the measures of projected future change from each modelling method and GCM were calculated (see section 4.1). The overall mean for each of these measures was also calculated, i.e. the mean values calculated from GAM (and all three GCM) and CRS (and all three GCM) averaged. Averages from climatic and SDM ensembles filter out biases of individual models and may provide a more accurate description of state (Araújo and New, 2006; Beaumont *et al.*, 2008). The measures of projected future change (see section 4.1) are future range extent (R), overlap (O), angle of range shift (θ), average geodesic range shift (D) and median minimum range shift (Dm; median of the minimum distances between present and future ranges), mean potential future species number per grid cell as a proportion of present number of species (N) and mean proportion of potential future species (relative to present) number per grid cell in overlap areas only (No). Alongside the mean, the 10^{th} and 90^{th} percentiles were calculated for all values (labelled, for example for R, as R_{10}-R_{90}).

Changes in range size based on number of grid cells could be problematic since latitude will affect the size of a grid cell (that one grid cell changes surface area with latitude). However, the forecast changes in species' range size from a number of studies (Chapter 2) indicate that changes in range size are likely to be greater in terms of number of grid cells than in the latitudinal shift. Breeding range shifts are expected to average 4° whilst non-breeding range shifts about 2° (Doswald *et al.* 2009). Furthermore, the ranges of the species modelled do not generally extend from the equator to the poles, where the most discernable distance would be seen. Comparing changes in breeding and non-breeding areas with one another may be problematic but is not undertaken here.

Potential average, minimum and maximum migration distances were also calculated. Average migration distance is the geodesic distance between the breeding and non-breeding range centroids. Minimum and maximum migration distances are the geodesic distances between the nearest and the furthest edges respectively. Unless otherwise specified all tables and figures represent the (overall) mean values. Results for individual species can be found in the digital appendices.

Wilcoxon's signed rank tests were performed between mean GAM and CRS to test for differences in overlap and extent between projections. Friedman tests were also conducted to test for differences in range overlap and extent between GCM modelled with both GAM and CRS. *Post hoc* Wilcoxon signed rank tests were conducted with Bonferroni corrections (the critical threshold for three comparisons is 0.0167). Effect sizes were calculated (see p. 75 and p.88), where appropriate, as described in Field (2005) and measure the magnitude of the observed effect. Effect sizes of 0.10 are small, 0.30 medium and 0.50 large (Field, 2005).

4.2.3 Results

Range extents

On average, species' distributions were projected to decrease in area on the breeding range and increase on the non-breeding range (Tables 4.10-4.11). In practice there was a large variation in relative range extent between species (digital appendix), methods and GCMs (Tables 4.12 – 4.17). Species' breeding ranges were more likely to decrease, with over 50% migrants losing range in the future. About 30 of the 229 species were projected to have less than 50% of climatically suitable range left in the future. About 62 species were projected to increase their climatically suitable breeding areas in the Western Palaearctic. On average, species' non-breeding ranges were projected to increase in the future with just over half of species' ranges increasing. About twenty species were simulated to lose more than half their non-breeding ranges, while another twenty species were simulated to double their climatically suitable area. Species' future ranges overlapped with their current range on average by half, though this varied once again (Tables 4.10-4.17). For 2025, about fifty out of 229 species were simulated to overlap with their current distribution (both ranges) by less than half. In 2085, this was the case for about 125 species.

Table 4.10: Multi-model mean summary of potential impacts on migrant bird's breeding range. Measures of changes between current and future simulations: R = relative change in range extent future/present O = proportion overlap future/present; D = range shift (km); Dm = minimum range shift (Km); θ = angle of change; N = Average species per grid cell with perfect dispersal; No = Average species per grid cell with dispersal failure. Values represent averages (e.g. R) and 10^{th} and 90^{th} percentile (e.g. R_{10}-R_{90})

	2025 A1B	2025 A2	2055 A1B	2055 A2	2085 A1B	2085 A2
R	0.98	0.98	0.96	0.95	0.96	0.97
R_{10}-R_{90}	0.50 - 1.23	0.51 - 1.19	0.40 - 1.22	0.40 - 1.30	0.40 - 1.36	0.38 - 1.42
O	0.68	0.69	0.56	0.57	0.49	0.47
O_{10}-O_{90}	0.32 - 0.88	0.32 - 0.90	0.19 - 0.82	0.22 - 0.83	0.15 - 0.78	0.14 - 0.76
D	419	405	577	563	701	744
D_{10}-D_{90}	148 - 903	136 - 888	238 - 1009	219 - 1011	306 - 1132	335 - 1194
Dm	136	135	195	183	231	247
Dm_{10}-Dm_{90}	50 - 200	50 - 190	309	53 - 299	61 - 442	61 - 465
θ	338.95	342.3	354.92	359.38	4.47	3.83
N	0.96	0.97	0.95	0.95	0.95	0.94
No	0.74	0.75	0.67	0.68	0.65	0.63

Table 4.11: Multi-model mean summary of potential impacts on migrant bird's non-breeding range. Measures of changes between current and future simulations: R = relative change in range extent future/present O = mean proportion overlap future/present; D = mean range shift (km); Dm = minimum range shift (Km); θ = mean angle of change; N = Average species per grid cell with perfect dispersal; No = Average species per grid cell with dispersal failure. Values represent averages (e.g. R) and 10^{th} and 90^{th} percentile (e.g. R_{10}-R_{90})

	2025 A1B	2025 A2	2055 A1B	2055 A2	2085 A1B	2085 A2
R	1.21	1.21	1.25	1.26	1.29	1.31
R_{10}-R_{90}	0.69 -1.89	0.69 - 1.94	0.56 - 1.89	0.56 - 1.89	0.50 - 1.94	0.51 - 2.00
O	0.68	0.69	0.58	0.59	0.52	0.49
O_{10}-O_{90}	0.36 - 0.91	0.37 - 0.91	0.18 - 0.86	0.20 - 0.86	0.15 - 0.86	0.10 - 0.84
D	665	638	908	896	1078	1147
D_{10}-D_{90}	154 - 1301	151 - 1278	258 - 1765	274 - 1750	364 - 1915	391 - 1906
Dm	194	181	323	310	411	429
Dm_{10}-Dm_{90}	17 - 279	19 - 275	30 - 546	28 - 495	42 - 857	49 - 884
θ	37.7	43.5	28	31.12	20.82	20.7
N	1.65	1.66	1.92	1.94	2.11	2.19
No	0.82	0.83	0.76	0.77	0.72	0.70

Mean future overlap with species' current ranges decreased through time and with more extreme emissions scenarios on both the breeding and non-breeding grounds regardless of the modelling method or GCM (Fig. 4.4a, c). Mean range extent showed a different pattern of change depending on the projected climate (Fig. 4.4 b, d). The GFDL projection gave rise to an increase in suitable climate on the breeding grounds and a decrease on the non-breeding grounds for migrant birds in 2085. The other GCMs simulated a gradual increase in potential range by 2085 on the non-breeding grounds and a decrease on the breeding grounds. A1B and A2 scenarios produced very similar results though A2 is a more extreme scenario.

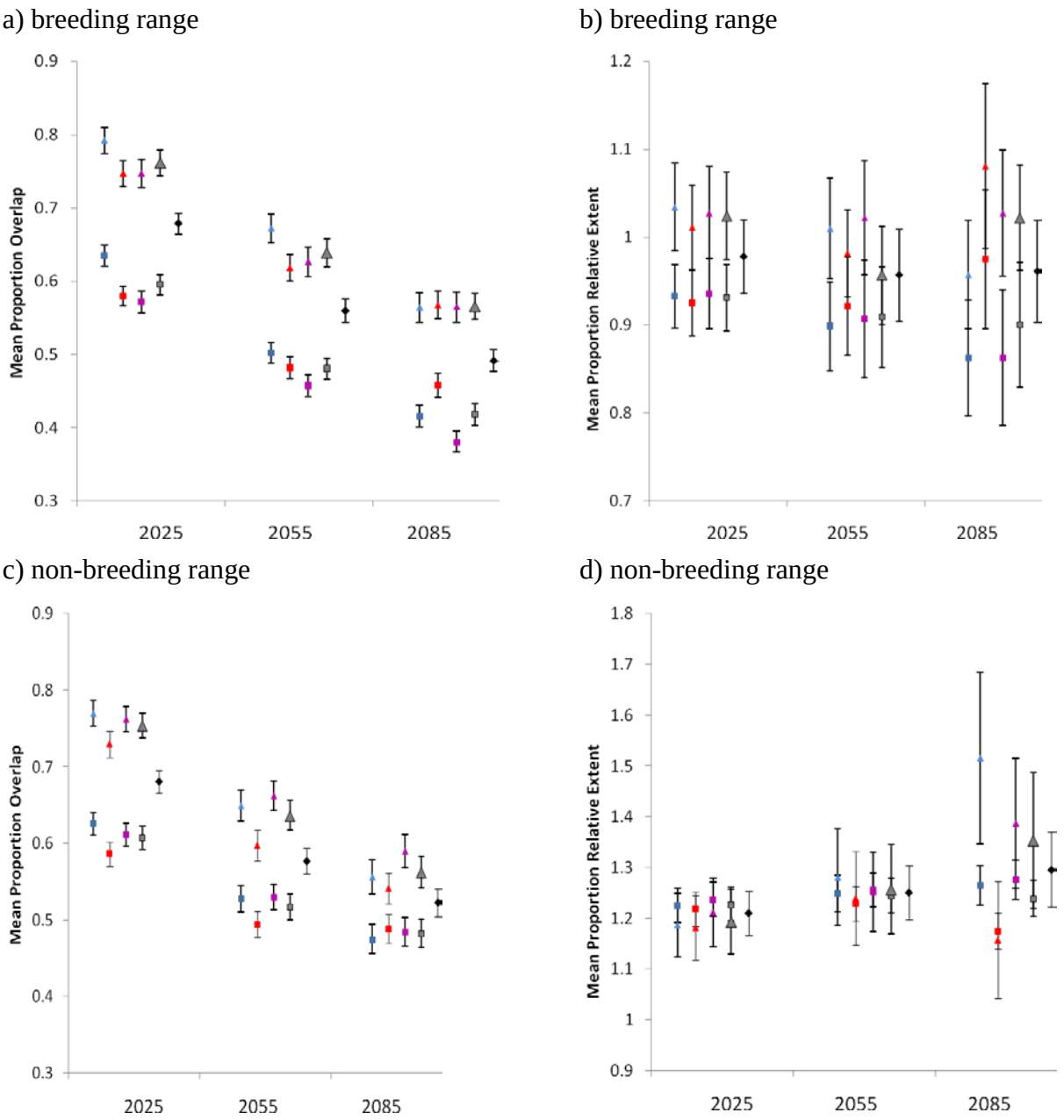


Figure 4.4: Change in overlap and relative range extent over time for the A1B scenario (A2 scenario found in Fig. A3; a) and c) mean proportion overlap of all migrants; b) and d) mean relative extent of all migrants; Triangles depict the GAM models and squares the CRS models. Blue represents Echam, red GFDL, and purple HadGEM. Grey are the model means while the black lozenges represent the multi-model mean value. Error bars represent standard error across species.

As Fig. 4.4 shows, GAM typically simulated higher overlap (O) and relative range extent (R) values than CRS though the patterns of change were in agreement with CRS models. Mean GAM O was significantly different to mean CRS O on both breeding and non-breeding grounds with high effect sizes in all time periods (Table A10). Mean GAM R was significantly different to mean CRS R on the non-breeding grounds in all time periods (Table A11). However, on the breeding grounds, there was no significant difference in R between mean GAM and mean CRS for the 2025 A2 scenario ($z = -1.838$, $p = 0.066$). There was a

significant difference for the other time periods though effect sizes were low for 2025, 2055 and marginally greater for 2085 (Table A11), suggesting GCM differences in prediction towards the end of the century. To test this theory, Wilcoxon signed rank tests with Bonferroni correction were performed to see the difference between GCMs (for each time period and scenario) on range extent values. These tests showed (Table A12) that GCMs were either similar ($p > 0.0167$) or, if significantly different, had very low effect sizes ($r < 0.30$). In terms of overlap all GCMs were different (Table A13).

Range shifts

The mean geodesic distance between centroids on the breeding ground ranged from 405 km in 2025 to 744 km in 2085 and on the non-breeding grounds from 638 km in 2025 to 1147 km in 2085 (Tables 4.10-11). This varied greatly among species, models and GCMs (Tables 4.12-4.17) though an increase in distance between centroids is obvious through time. Tables 4.10 to 4.17 also give the average median minimum distance (average Dm) required for a species to move to the new suitable climate. These distances also increased through time and ranged from 135 km and 191 km in 2025 for the breeding and non-breeding grounds respectively to 247 km and 429 km in 2085.

The average angle of shift for migrants' breeding and non-breeding ranges was projected to be in a northerly direction (Tables 4.10-4.17). However, the actual mean values do not fully reflect the variation present among species (Fig. 4.14-4.19 in section 4.3.3 and Appendix IIIc). For 2025 and 2055, GAM and CRS showed a difference in species' direction of shift on the breeding range, with more species moving north-west according to the CRS models and species moving north-east according to GAM models. In 2085, however, both modelling methods simulated a north-eastern shift in centroid. GAM and CRS predictions were more similar for the non-breeding grounds.

Theses differences/similarities can be seen by viewing the simulated species richness maps (Fig. 4.6 and 4.7) and the simulated future maps in the digital appendix. Direction of shift in range was related to the mean latitude of species' ranges (Figure 4.5 and digital appendix).

Table 4.12: Summary of potential impacts of climate change on migrant birds for 2025 on their breeding range. See Table 4.10 for abbreviations.

2025	A1B emissions scenario						A2 emissions scenario					
	GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
R	1.01	0.93	1.03	0.93	1.03	0.94	1.03	0.94	1.03	0.93	1.01	0.94
R_{10}-R_{90}	0.34-1.40	0.51-1.27	0.32-1.34	0.51-1.19	0.28-1.42	0.46-1.26	0.34-1.33	0.51-1.22	0.28-1.32	0.54-1.11	0.28-1.31	0.45-1.26
O	0.75	0.58	0.79	0.64	0.75	0.57	0.77	0.61	0.79	0.64	0.74	0.58
O_{10}-O_{90}	0.26-0.97	0.27-0.80	0.27-0.99	0.32-0.87	0.22-0.98	0.23-0 82	0.31-0.97	0.32-0.83	0.25-0.99	0.33-0.87	0.24-0.97	0.22-0.82
D	431	413	384	387	448	444	418	400	379	368	441	423
D_{10}-D_{90}	81-1010	131-875	47-1045	101-774	78-1018	153-830	62-999	125-780	44-1029	99-761	78-1009	146-818
Dm	131	135	140	112	163	132	155	120	130	111	152	129
Dm_{10}-Dm_{90}	50-168	50-189	50-181	50-146	50-163	50-201	50-182	50-164	50-167	50-121	50-193	50-199
θ	7.63	321.31	356.97	314.78	10.11	318.54	7.83	317.65	8.02	312.36	14.71	325.30
N	0.90	0.99	0.93	1.02	0.94	1.00	0.93	1.00	0.93	1.01	0.93	1.00
No	0.77	0.69	0.80	0.72	0.78	0.70	0.79	0.72	0.80	0.73	0.77	0.69

Table 4.13: Summary of potential impacts of climate change on migrant birds for 2025 on their non-breeding range. See Table 4.10 for abbreviations.

2025	A1B emissions scenario						A2 emissions scenario					
	GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
R	1.81	1.21	1.19	1.23	1.21	1.24	1.2	1.24	1.2	1.23	1.2	1.22
R_{10}-R_{90}	0.49-1.77	0.71-1.87	0.50-1.76	0.73-1.90	0.50-1.82	0.70-1.98	0.49-1.83	0.72-1.88	0.53-1.84	0.74-1.90	0.51-1.83	0.69-1.94
O	0.73	0.59	0.77	0.63	0.76	0.61	0.75	0.61	0.78	0.64	0.76	0.61
O_{10}-O_{90}	0.32-0.97	0.34-0.86	0.39-0.97	0.29-0.88	0.37-0.98	0.26-0.97	0.32-0.97	0.25-0.87	0.41-0.98	0.30-0.89	0.39-0.97	0.27-0.87
D	707	666	660	588	692	655	680	626	624	565	702	625
D_{10}-D_{90}	76-1452	141-1282	58-1520	114-1198	86-1476	157-1283	71-1392	146-1207	56-1348	115-1133	76-1531	158-1287
Dm	187	221	169	194	151	212	204	196	137	170	157	208
Dm_{10}-Dm_{90}	0-221	0-332	20-221	1-319	48-221	1-348	49-234	0-334	47-193	1-312	49-221	1-333
θ	47.57	35.84	36	54.73	29.91	23.67	48.32	52.96	41.03	57.38	32.91	39.32
N	1.27	2.41	1.22	2.38	1.27	2.44	1.27	2.31	1.25	2.56	1.31	2.45
No	0.56	0.74	0.87	0.75	0.86	0.74	0.87	0.76	0.89	0.77	0.86	0.733

Table 4.14: Summary of potential impacts of climate change on migrant birds for 2055 on their breeding range. See Table 4.10 for abbreviations.

	A1B emissions scenario						A2 emissions scenario					
2055	GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
R	0.98	0.92	1.00	0.90	1.02	0.91	0.98	0.91	0.99	0.92	0.99	0.92
R_{10}-R_{90}	0.32-1.37	0.41-1.34	0.25-1.35	0.40-1.68	0.22-1.40	0.32-1.28	0.31-1.30	0.37-1.30	0.29-1.38	0.38-1.36	0.23-1.38	0.31-1.36
O	0.62	0.48	0.67	0.50	0.63	0.46	0.64	0.50	0.67	0.52	0.62	0.46
O_{10}-O_{90}	0.21-0.91	0.14-0.75	0.16-0.94	0.18-0.76	0.08-0.93	0.10-0.73	0.21-0.91	0.16-0.76	0.20-0.94	0.16-0.79	0.09-0.93	0.11-0.75
D	629	542	544	493	677	566	594	502	539	488	665	586
D_{10}-D_{90}	202-1284	209-968	145-1136	192-939	191-1402	225-1030	166-1229	184-929	132-1133	173-920	183-1308	228-1080
Dm	175	182	178	160	246	201	139	169	178	160	230	200
Dm_{10}-Dm_{90}	50-251	50-295	50-228	50-222	50-462	50-322	50-210	50-251	50-237	50-235	50-510	50-315
θ	11.25	342.92	12.13	333.69	10.29	336.45	16.4	342.41	17.18	339.54	12.5	338.61
N	0.88	0.93	0.93	0.98	0.97	0.98	0.88	0.95	0.93	0.98	0.96	0.98
No	0.7	0.612	0.73	0.65	0.71	0.63	0.71	0.63	0.74	0.65	0.71	0.62

Table 4.15: Summary of potential impacts of climate change on migrant birds for 2055 on their non-breeding range. See Table for abbreviations.

	A1B emissions scenario						A2 emissions scenario					
2055	GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
R	1.24	1.23	1.28	1.25	1.25	1.26	1.25	1.25	1.3	1.25	1.25	1.26
R_{10}-R_{90}	0.33-1.96	0.61-1.95	0.36-1.88	0.65-1.90	0.40-1.76	0.66-1.96	0.37-1.97	0.61-1.99	0.39-1.88	0.62-1.98	0.36-1.86	0.67-2.02
O	0.60	0.49	0.65	0.53	0.66	0.53	0.62	0.51	0.67	0.54	0.65	0.53
O_{10}-O_{90}	0.10-0.93	0.11-0.80	0.19-0.96	0.13-0.86	0.23-0.97	0.13-0.85	0.14-0.93	0.14-0.81	0.20-0.97	0.15-0.86	0.22-0.95	0.16-0.83
D	994	907	905	899	862	865	931	884	895	877	916	847
D_{10}-D_{90}	156-2125	254-1617	104-2018	274-1832	108-1787	251-1705	142-2054	254-1624	114-2047	274-1727	142-1957	265-1511
Dm	328	308	288	352	280	337	278	307	276	320	290	318
Dm_{10}-Dm_{90}	0-578	1-524	46-411	1-554	49-412	40-542	0-403	1-497	49-350	1-546	48-434	45-513
θ	40.05	30.71	27.08	27.10	31.75	27.63	40.05	30.71	27.08	27.11	31.73	27.63
N	1.49	2.86	1.41	2.83	1.48	2.85	1.52	2.86	1.47	2.80	5.51	2.84
No	0.78	0.69	0.81	0.70	0.81	0.69	0.80	0.70	0.82	0.71	0.80	0.69

Table 4.16: Summary of potential impacts of climate change on migrant birds for 2085 on their breeding range. See Table 4.10 for abbreviations.

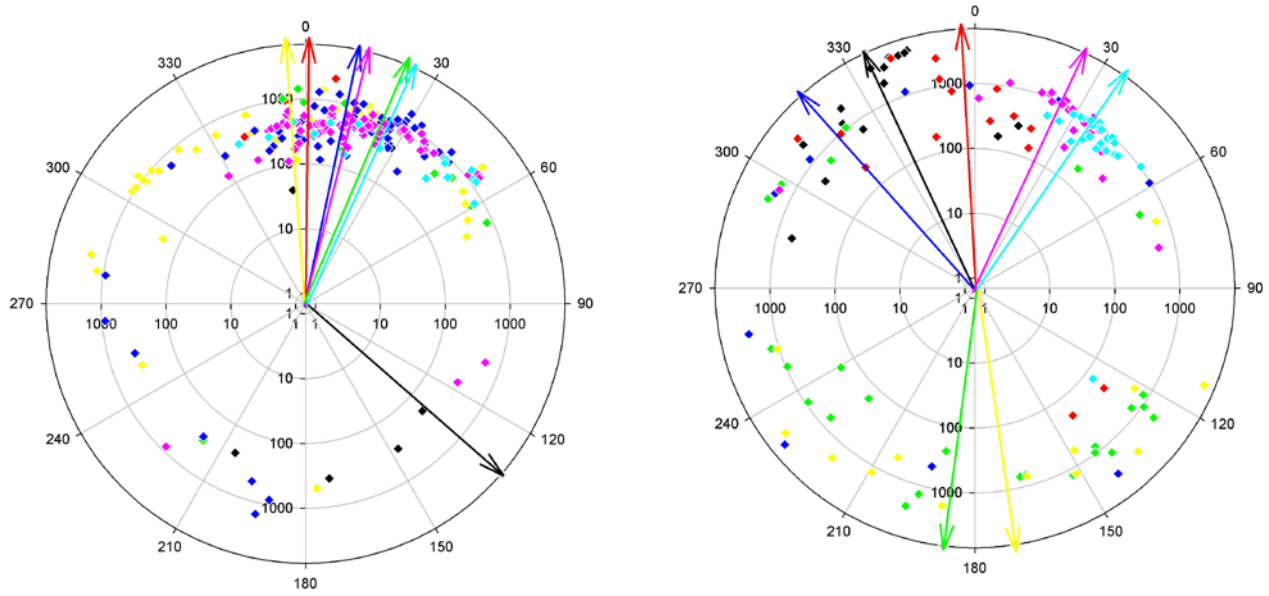
	A1B emissions scenario						A2 emissions scenario					
2085	GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
R	1.08	0.97	0.96	0.862	1.02	0.86	1.15	0.99	0.96	0.86	1.01	0.86
R_{10}-R_{90}	0.34-1.60	0.41-1.35	0.18-1.40	0.29-1.32	0.19-1.55	0.26-1.36	0.30-1.67	0.39-1.40	0.17-1.40	0.28-1.39	0.14-1.60	0.19-1.43
O	0.57	0.46	0.56	0.42	0.56	0.38	0.55	0.45	0.55	0.41	0.51	0.35
O_{10}-O_{90}	0.16-0.89	0.08-0.76	0.05-0.90	0.07-0.71	0.03-0.90	0.05-0.66	0.14-0.88	0.07-0.74	0.06-0.89	0.08-0.70	0.02-0.88	0.02-0.64
D	667	640	748	625	826	693	706	662	783	627	922	762
D_{10}-D_{90}	230-1097	243-1079	225-1513	241-1091	257-1568	317-1263	253-1205	257-1147	257-1563	246-1090	318-1709	341-1351
Dm	189	224	235	203	269	238	194	231	232	208	324	273
Dm_{10}-Dm_{90}	50-367	67-470	50-362	50-386	50-560	51-488	50-400	63-462	50-360	50-389	50-689	50-573
θ	21.27	11.76	17.03	347.09	9.18	335.9	18.62	9.26	15.17	348.53	8.96	339.61
N	0.91	0.94	0.93	0.95	1.00	0.98	0.91	0.94	0.93	0.95	0.99	0.95
No	0.72	0.63	0.66	0.59	0.67	0.59	0.71	0.63	0.67	0.58	0.64	0.55

Table 4.17: Summary of potential impacts of climate change on migrant birds for 2085 on their non-breeding range. See Table 4.10 for abbreviations.

	A1B emissions scenario						A2 emissions scenario					
2085	GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
R	1.15	1.18	1.51	1.26	1.39	1.28	1.21	1.17	1.54	1.27	1.4	1.27
R_{10}-R_{90}	0.29-1.78	0.55-1.83	0.26-2.36	0.52-2.07	0.29-2.17	0.50-2.05	0.25-1.90	0.52-1.93	0.25-2.43	0.47-2.17	0.25-2.25	0.55-2.03
O	0.54	0.49	0.56	0.48	0.59	0.48	0.50	0.47	0.54	0.47	0.54	0.46
O_{10}-O_{90}	0.10-0.93	0.10-0.85	0.04-0.95	0.05-0.84	0.11-0.97	0.09-0.84	0.05-0.92	0.06-0.86	0.03-0.95	0.04-0.84	0.09-0.95	0.08-0.83
D	962	977	1223	1193	1064	995	1085	1052	1262	1170	1178	1099
D_{10}-D_{90}	200-2055	228-1823	201-2675	374-2161	156-2151	323-1607	213-2330	257-1951	202-3042	399-1931	221-2332	359-1968
Dm	425	363	400	444	365	369	465	396	432	407	385	415
Dm_{10}-Dm_{90}	50-962	71-653	0-913	49-827	1-748	50-671	50-957	81-755	0-981	50-757	0-852	28-688
θ	39.59	20.18	11.08	15.04	11.55	21.06	31.84	19.71	17.13	21.03	17.48	17.14
N	1.34	2.48	1.79	3.26	1.62	3.20	1.41	2.58	1.81	3.29	1.78	3.35
No	0.73	0.65	0.77	0.67	0.77	0.67	0.72	0.64	0.46	0.66	0.74	0.64

a) CRS simulation

b) CRS simulation



c) GAM simulation

d) GAM simulation

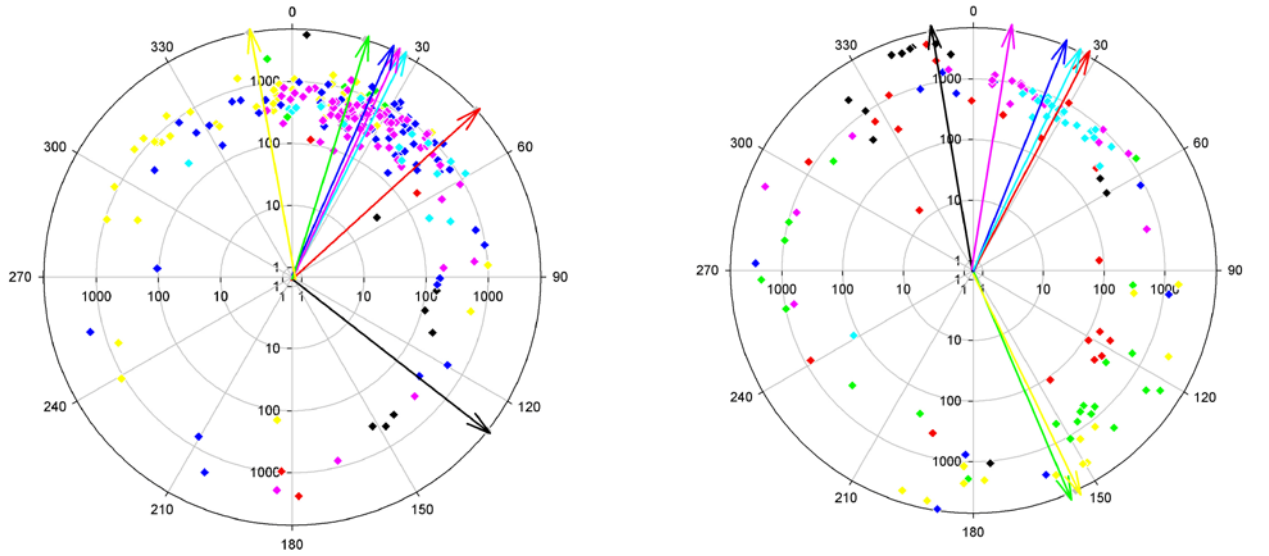


Figure 4.5: Direction and distance of shift of species ranges from GFDL 2085 A1B scenario by latitude of centroid; a) and c) breeding range – black: 1°-10°, red: 11°-20°, green: 21°-30°, yellow: 31°-40°, dark blue: 41°-50°, pink: 51°-60° and light blue: 61°-70°; b) and d) non-breeding range (with species with split range excluded see section 4.3) – black: -22°- -11°, red: -10°-1°, green: 2°-11°, yellow: 12°-21°, dark blue: 22°-31°, pink: 32°-41° and light blue: 42°-52°.

Species richness

The changes in range extent influence the projections of local avian species richness across Europe and Africa (N values in Tables 4.10-4.17), so that species richness during the breeding season was projected to decrease, on average, owing to decreased extent of climatically suitable areas. On the non-breeding grounds the models predicted an increase in species richness brought about by increased extent of climatically suitable areas. On average, the simulations projected a decrease of 5% of species per grid cell on the breeding range and a 90% increase on the non-breeding grounds. However, if species cannot disperse to new areas and persist only in their current ranges then species richness is projected to decrease by 30% on average on both ranges. Figure 4.6-4.7 shows the multi-model mean species richness in the present and future A1B scenario (the A2 scenario can be found in Appendix III b). The bulk of species are simulated to shift their ranges northwards in Europe and retreat from southern Europe (Fig. 4.6). African breeding migrants dwindle in numbers over time. During the non-breeding season (Fig. 4.7), the models projected that species' numbers would increase in central and northern Europe, as well as in the Sahel region but decrease in number in South Africa. Both figures, however, show the decreases in species' numbers in case of 'dispersal failure' (Fig 4.6 and 4.7 c, e, g).

In Fig 4.8 a) and b), the variance of the current consensus model (GAM and CRS) is shown and quantifies the differences between simulations. The models varied mostly around the Mediterranean coast and Turkey as well as eastern Africa in the non-breeding models. The variation in the future models (Fig 4.8), in regions other than those aforementioned, is likely to be due to GCM and interactions between GCM and models. These spatially quantify the uncertainty surrounding the projections. For the breeding season models, variation increased dramatically all over Europe through time as well as in Africa. For the non-breeding models, variation also increased through time.

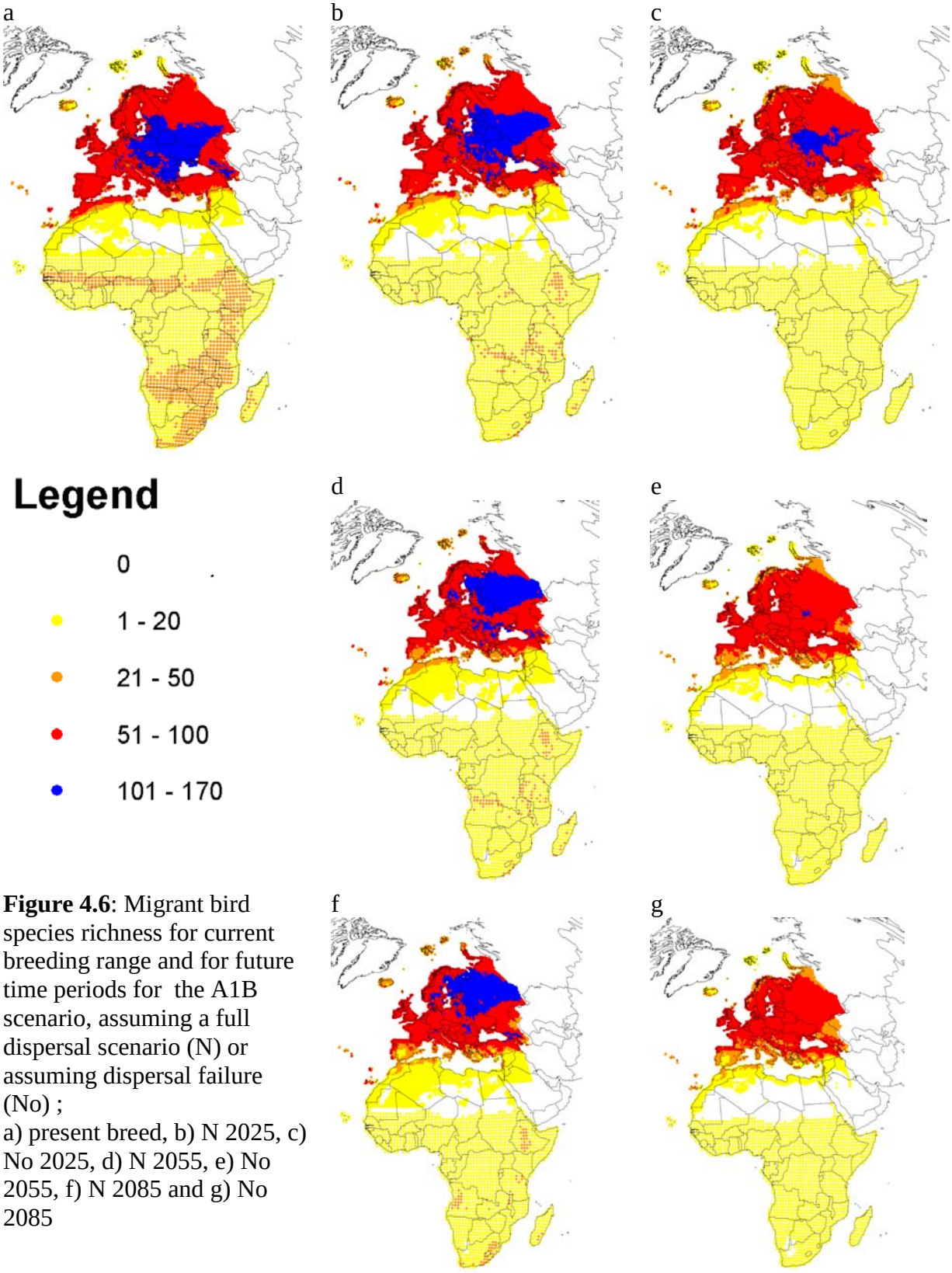


Figure 4.6: Migrant bird species richness for current breeding range and for future time periods for the A1B scenario, assuming a full dispersal scenario (N) or assuming dispersal failure (No) ;
a) present breed, b) N 2025, c) No 2025, d) N 2055, e) No 2055, f) N 2085 and g) No 2085

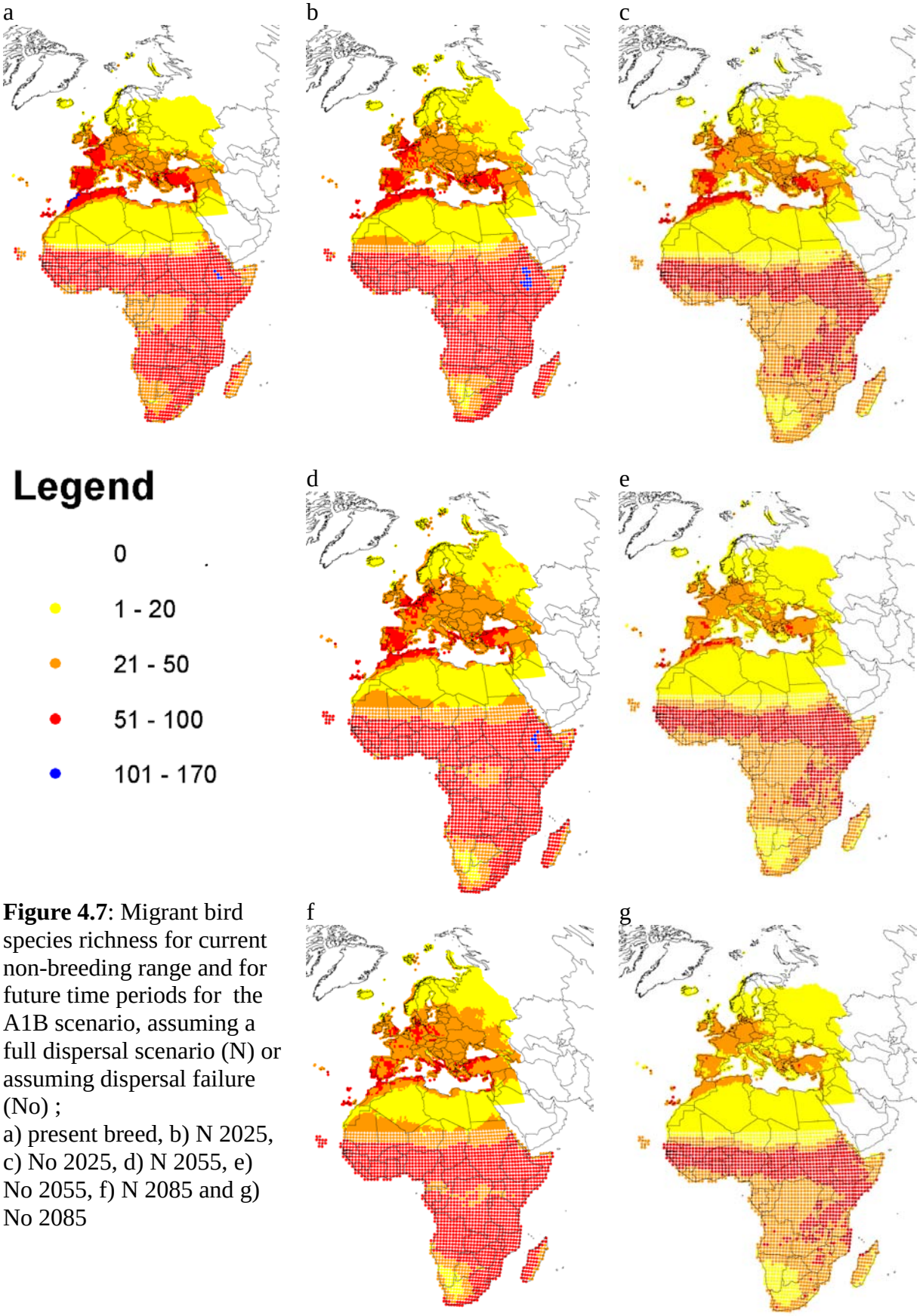


Figure 4.7: Migrant bird species richness for current non-breeding range and for future time periods for the A1B scenario, assuming a full dispersal scenario (N) or assuming dispersal failure (No) ;
a) present breed, b) N 2025, c) No 2025, d) N 2055, e) No 2055, f) N 2085 and g) No 2085

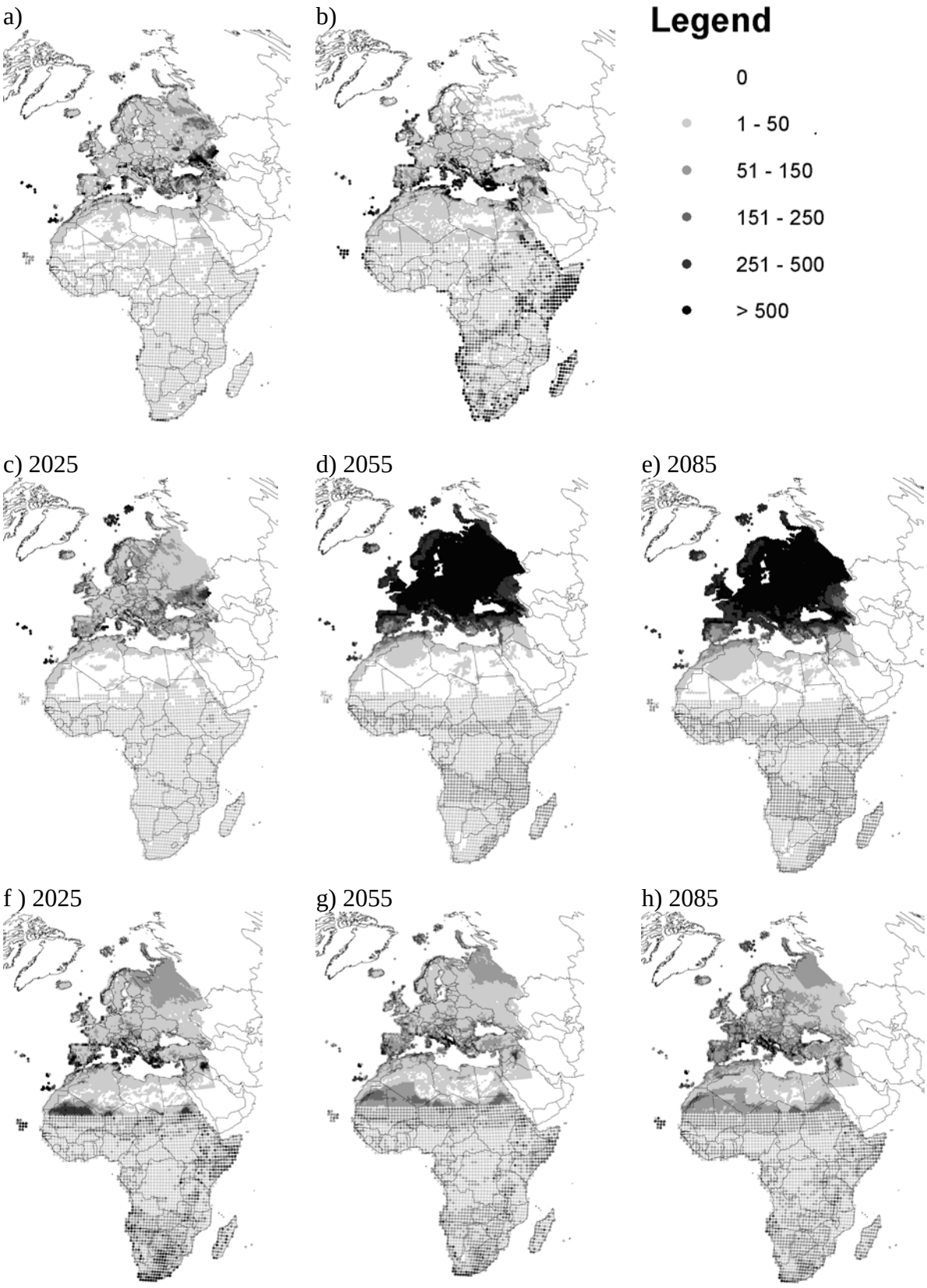


Figure 4.8: Variance of mean species richness (N) from the consensus models for current; a) breeding models, b) non- breeding models; and future (2025, 2055, 2085) A1B scenario; c,d,e) breeding models and f,g,h) non-breeding models.

Migratory distance

Average simulated current 'migration distance' is shown in table 4.18. Average migration distances are projected to increase in the future (Table 4.19 and summarised in Fig. 4.9). There are differences in prediction of migration distances towards the end of the century between GCMs (Fig 4.9), which stems from the increases in non-breeding range extent (Fig. 4.4). Migration distance was greater using the GAM methods than CRS.

Table 4.18: Average migration distance (M), Minimum and Maximum migration distance (Mmin & Mmax) in Km for the present time period as projected by GAM and CRS methods. The 10^{th} and 90^{th} percentile values are also reported.

	GAM	CRS
M	3346	3211
M_{10}-M_{90}	717-6204	523-6528
Mmin	1049	918
$Mmin_{10}$-$Mmin_{90}$	0-3299	0-3306
Mmax	8426	8532
$Mmax_{10}$-$Mmax_{90}$	6322-9919	7133-9858

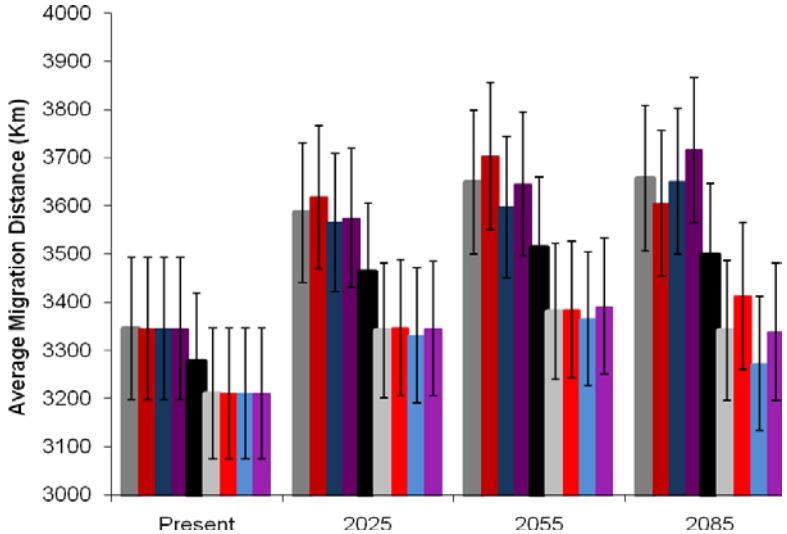


Figure 4.9: Average mean migration distance (Km) through time for the A1B scenario. The A2 scenario shows the same pattern (Fig. A4). Grey represents the model mean, black the multi-model mean, red represents GFDL, blue Echam and purple HadGEM. Dark colours represent GAM and light colours CRS. Error bars represent standard error across species.

On average, minimum migration distances are projected to decrease slightly through time (Table 4.19). Four sample trans-Saharan migrant species' future distribution maps in Figure 4.10 illustrate how migration distances may be reduced. Some species are projected to gain suitable wintering areas on the North African coast (e.g. Fig 4.10 a, e, b and f), while *Acrocephalus arundinaceus*, for instance, is predicted to gain suitable wintering areas in the Mediterranean (Fig. 4.10 c and g).

Maximum migration distance is simulated to increase in future change scenarios (Table 4.19). Figure 4.10 b, f, d and h illustrate how an expansion North on the breeding grounds and/or an expansion South on the non-breeding grounds may cause greater migration distances. The figures also show the diversity in species' potential range changes that summary statistics for all species do not fully capture.

Table 4.19: Average migration distance (M), relative change in migration distance (Pm) and minimum and maximum migration distance in Km. 10th and 90th percentiles are also given (M_{10}-M_{90}).

		A1B emissions scenario						A2 emissions scenario					
		GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
		GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
2025	M	3618	3348	3566	3331	3575	3346	3585	3363	3533	3306	3560	3336
	M_{10}-M_{90}	696-6711	716-6208	668-6541	767-6172	760-6514	820-6290	700-6558	700-6276	660-6443	769-6185	709-6538	717-6121
	Pm	1.51	1.26	1.48	1.26	1.49	1.27	1.45	1.26	1.46	1.23	1.47	1.28
	Pm_{10}-Pm_{90}	0.64-1.57	0.83-1.69	0.65-1.62	0.81-1.61	0.67-1.69	0.81-1.61	0.64-1.53	0.82-1.72	0.64-1.58	0.82-1.58	0.59-1.67	0.83-1.61
	Mmin	1102	720	1040	738	980	691	1028	764	1026	773	987	682
	$Mmin_{10}$-$Mmin_{90}$	0-3349	0-2699	0-3171	0-2606	0-3026	0-2500	0-3096	0-2771	0-3046	0-2619	0-3190	0-2516
	Mmax	8338	8912	8340	8854	8327	8903	8300	8922	8345	8687	8349	8939
	$Mmax_{10}$-$Mmax_{90}$	5764-9928	7708-9949	5948-9938	7559-9939	5725-9955	7678-9958	5706-9945	7817-9962	5980-9939	7535-9682	6057-9947	7859-9961
2055	M	3703	3385	3598	3366	3646	3392	3622	3354	3569	3338	3628	3371
	M_{10}-M_{90}	529-6800	680-6214	680-6483	709-6224	678-6581	717-6221	636-6552	657-6190	708-6461	692-6206	723-6490	704-6243
	Pm	1.56	1.29	1.52	1.28	1.55	1.27	1.53	1.27	1.478	1.26	1.55	1.27
	Pm_{10}-Pm_{90}	0.53-1.74	0.72-1.86	0.60-1.76	0.71-1.98	0.57-1.69	0.74-1.79	0.54-1.67	0.71-1.76	0.61-1.645	0.71-1.85	0.57-1.66	0.72-1.71
	Mmin	1026	634	966	607	943	527	1010	667	979	600	919	493
	$Mmin_{10}$-$Mmin_{90}$	0-3515	0-2717	0-3187	0-2699	0-3105	0-1814	0-3346	0-2810	0-3193	0-2522	0-3062	0-1702
	Mmax	8420	9045	8431	8996	8433	9037	8399	8966	8430	8987	8484	9096
	$Mmax_{10}$-$Mmax_{90}$	5564-9961	7996-9967	6084-9948	7841-9962	5935-9963	7891-9971	5835-9947	7723-9836	6071-9944	7861-9968	6270-9970	7978-9972

		A1B emissions scenario						A2 emissions scenario					
		GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
Table 4.19 continued		GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
2085	M	3606	3413	3651	3273	3716	3339	3503	3430	3701	3265	3721	3302
	M_{10}-M_{90}	755-6455	591-6666	664-6714	639-6164	671-6685	720-6283	696-6580	591-6704	656-6698	652-6171	579-6605	740-6158
	Pm	1.14	1.16	1.57	1.27	1.61	1.31	1.11	1.08	1.58	1.26	1.65	1.32
	Pm_{10}-Pm_{90}	0.75-1.53	0.62-1.64	0.53-1.86	0.62-1.85	0.58-1.92	0.66-1.85	0.69-1.48	0.54-1.50	0.53-1.91	0.62-1.75	0.55-1.94	0.61-1.97
	Mmin	945	514	850	457	872	427	799	461	919	517	846	413
	$Mmin_{10}$-$Mmin_{90}$	0-3664	0-2143	0-3021	0-1570	0-3180	0-1514	0-2777	0-1788	0-3205	0-2011	0-2891	0-1449
	Mmax	8494	9007	8453	9088	8462	9118	8225	9020	8473	9106	8459	9182
	$Mmax_{10}$-$Mmax_{90}$	6085-9953	7827-9978	5798-9954	7944-9973	5709-9962	8035-9972	3985-9968	7872-9977	5560-9963	7913-9976	5602-9974	8147-9975

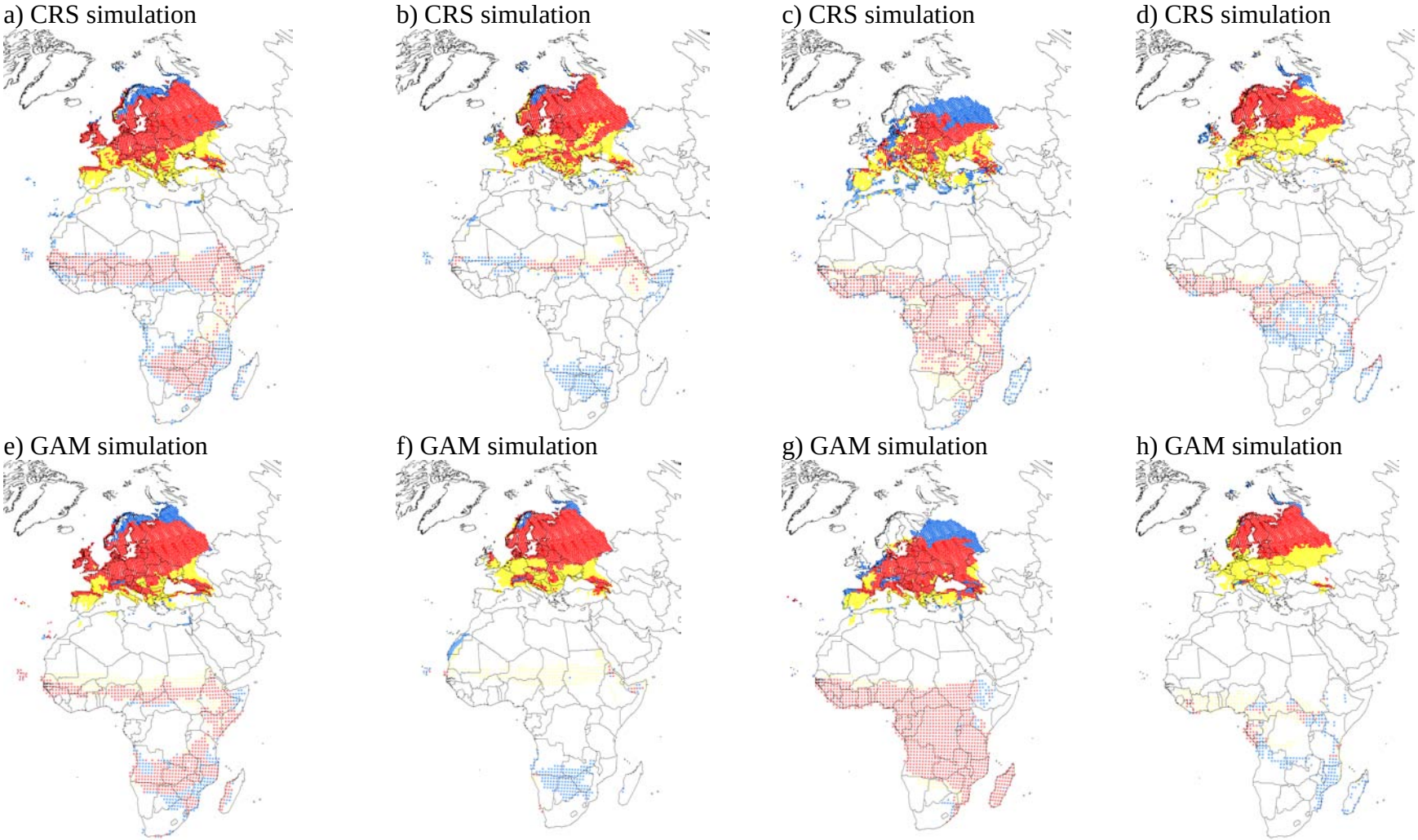


Figure 4.10: Future range change for individual species under GFDL 2085 A1B scenario – Blue = future range only, Yellow = current range only, Red = overlapping ranges; darker colours are for breeding range; a) and e) *Sylvia communis* (Whitethroat); b) and f) *Sylvia curruca* (Lesser Whitethroat); c) and g) *Acrocephalus arundinaceus* (Great Reed Warbler); d) and h) *Ficedula hypoleuca* (Pied Flycatcher).

4.2.4 Discussion

This study shows how climate change might impact European breeding migrant birds in relation to their breeding and non-breeding distributions, and resultant migration distances. In general the future simulations project differential change in the European breeding distribution to the non-breeding distribution: on the breeding grounds, a decrease in climate suitability and a northwards shift in range; on the non-breeding grounds, range expansion (as a result of increased climate suitability) but at a greater distance from the original range, with a shift eastwards in the core ranges of the majority of species.

This study also highlights the variation in how species are likely to respond to climate change. Species will respond individualistically, as many researchers have already projected (Huntley *et al.*, 2006; Devictor *et al.*, 2008). However, individual species' responses as predicted by climate envelope modelling may be incorrect or nonsensical since climate envelope modelling does not take into account land use, demography or historical factors. I, therefore, concentrate in the first instance on reporting the mean response of a group of species. Taking the mean response from a large number of species as well as from a 'consensus multi-model forecast' increases the robustness of predictions of the likely magnitude and direction of potential change for European migrant birds (Huntley *et al.*, 2008).

GAM and CRS simulated a similar direction of change but depicted different magnitudes of change. GAM projected on average greater relative range extent and migration distance values than CRS on both the breeding and non-breeding ranges. This difference potentially stems from how they relate climate to occurrences. With the uncertainty surrounding the modelling (Barry and Elith, 2006), taking the mean forecast is a sensible approach (Thuiller, 2004; Araújo and New, 2006).

In terms of GCM, my results for the breeding range shifts were the same as Huntley *et al.* (2008) in that there was a significant variation in overlap among GCM but not in relative range extent. This variation highlights that the different GCMs simulate different patterns of climatic change. Differences between GCM interacting with modelling method may also reflect that the models project onto novel climates.

Distribution change

The models project that, on average, migrant birds' range extents are likely to decrease by 2-5% on the breeding grounds and increase by 20-30% on the non-breeding range. However, potential changes in range extent are misleading as species may not expand into the newly suitable climate space either because of availability of suitable habitat or simply distance or because of historical and genetic factors. For example *Sylvia melanothorax*, which is endemic to Cyprus, is unlikely to expand its range (Böhning-Gaese *et al.*, 2003; Böhning-Gaese *et al.*, 2006). Percentage overlap between current and future suitable climate is potentially a more 'accurate', albeit pessimistic, predictor of climatic impacts. The models predicted that, on average, 50% of original range is still suitable in the future for both the breeding and non-breeding ranges. The models projected that by 2085 over half the migrants modelled will have less than half their current range. These values are similar to other studies (e.g. Huntley *et al.*, 2008).

Changes through time are simulated to be linear for most species, with a progressive loss or gain of range. However, some species are simulated to exhibit a non-linear response. This is most notable in terms of relative range extent (Fig. 4.4b) with a simulated decrease in range at first then an increase towards the end of the century. These distinctions in shape of response over time were also simulated for breeding birds in Britain and Ireland by Harrison *et al.* (2003). They found species either progressively lost/gained climate space or exhibited non-linear responses to climate change. Such results highlight that responses to climate change may be complex.

Species richness of migrants was predicted to decrease on the breeding grounds and increase on the non-breeding grounds. However, if species do not expand into new climate space, then species richness is forecast to decrease by about 30% on both ranges. On the breeding grounds most migrants are expected to shift their ranges northwards in Europe or dramatically contract their ranges. For those European migrant species that have populations that breed in Africa, area is gradually lost from East Africa. On the non-breeding grounds, species' numbers per grid cell dwindle in Europe over time. Average number per grid cell in Africa, however, is predicted to increase under the full dispersal scenario in central, western and the eastern coast and decrease in South Africa. Under the no dispersal scenario numbers are reduced everywhere. Changes in breeding migrant bird richness in relation to overall breeding bird richness across Europe were investigated by Schaefer *et al.* (2008). Their simulated results suggest that, under climate change forecasts, proportion of migrant species would increase in southern Europe due to

community reassembly and decrease in the north due to adaptation. They concluded that climate change affect migrants less severely than resident species. I investigate this further section 4.3.

Range shifts and dispersal

The geodesic distance values calculated between current and future centroids of species' ranges show how much species' ranges might shift under a scenario of perfect dispersal. Shifts were simulated to be greater on the non-breeding grounds. Range shifts are expected to increase through time by several hundreds of Kms between each time period. Devictor *et al.* (2008) have shown that although birds have already shifted their ranges in response to climate change in Europe, species are lagging approximately 182 ± 53 km behind climate change. The sometimes large predicted future shifts in climate suitability may therefore considerably increase this lag.

GAM models simulated a greater shift than for CRS. There were also consistent differences between GCM. Greater shifts were simulated by HadGEM on the breeding grounds and by GFDL on the non-breeding grounds. The HadGEM GCM simulated higher future temperatures in Europe, whilst GFDL exhibited greater differences in future climate projections in Africa (more precipitation and different temperature distribution) than the multi-model mean (Solomon *et al.* 2007). The shifts were generally simulated to be in a northerly direction in Europe. Potential shifts in Africa were more complex and related to the mean latitude of species' current distributional range (Fig. 4.5).

If a species can disperse into new climate space, the models project, on average, an increased distance of hundreds of Km between current and future suitable range. Even though birds are highly mobile species, colonising new range may be limited by dispersal and phenotypic plasticity. The average natal dispersal distance for migrants is 22.8 km for migrants with a range of 0.7-44.5 km for all birds (Paradis *et al.*, 1998). Limited natal dispersal may create a lag behind the projected changes. On the other hand, a few individuals within a population will have longer dispersal distances than the average; and it is often these individuals that drive colonisation (Newton, 2003). The distances between current and future suitable range are greater on the non-breeding grounds. Many migrant birds are semi-nomadic on their non-breeding grounds (Berthold, 2001), often following rainfall (Jones *et al.*, 1996; Salewski and Jones, 2006) which might reduce this impact. On the other hand some species are known to be faithful to their non-breeding sites (Markovets and Yosef, 2005).

The Sahara and Mediterranean represent major obstacles to shifts in species' ranges. These obstacles increase the distances between present and future suitable climate. They may also exacerbate conditions if migratory distance increases because of reduced possibilities to refuel during crossing of the Sahara desert and Mediterranean Sea. In other migratory systems, changes to species' migratory distance may be lessened without these obstacles. Further, absence of obstacles would allow for a more continued habitat to be available for range change. The generality of the results for migratory birds from this thesis may, therefore, be limited. Other migratory systems would have to be evaluated in their own right to establish climate change impacts on migratory species in different systems.

Migration

Changes in range extent and position also affect how far an obligate migratory species will have to migrate between breeding and non-breeding grounds. The migration distance values calculated do not represent the 'true' migration distances for each species, but the geodesic distances between two points. Real migration distances could not be calculated as 1) different populations of a species migrate different distances, 2) some species exhibit non-linear migration routes and 3) I did not have exact distance information for different species. My results showed that average migration distance increases steadily from the present to 2055 then stabilises. However, some species are simulated to reduce their average migratory distance by 2085. This potential reduction in migration distance is the result of the non-breeding areas extending closer to the breeding grounds. Generally, the models simulated a reduction in minimum migratory distance and an increase in maximum migratory distance.

Increases in maximum migration distance may not necessarily be realised. Reduced minimum or mean migratory distance is due to newly suitable non-breeding climate space occurring closer to the breeding grounds. There is currently evidence of some species over-wintering closer to their breeding grounds (Valiela and Bowen, 2003; Austin and Rehfisch, 2005) as milder winters in Europe allow species to migrate less (Austin and Rehfisch, 2005) or become sedentary (Coppack *et al.*, 2003). Potential changes in migratory behaviour are discussed in the next section.

4.2.5 Conclusion

The potential impacts on European breeding migrant birds are likely to be complex, with different factors operating on the breeding and non-breeding grounds. The simulated differences on the seasonal ranges make interpretation of the potential impact difficult, because the resultant effects can not be as uncoupled as the measures calculated. For instance, climatic suitability is likely to decrease on the breeding range according to the simulations but increase on the non-breeding grounds. An increase on the non-breeding grounds is unlikely to affect species positively if increased mortality ensues from decreased suitability during the breeding season. Conversely, decreased suitability on the breeding grounds may be offset with a greater proportion of species surviving the 'winters' on the non-breeding grounds, or from having to travel less far.

The predicted impacts of climate change are, furthermore, likely to be underestimated in terms of population change, since although range is often used as a correlate of population size (Rodrigues *et al.*, 2006), species do not fully occupy the current or projected ranges (Shoo *et al.*, 2005; Jetz *et al.*, 2007), especially the climatic ranges built on broad atlas data (Jetz *et al.*, 2008). Moreover, future impacts on species' distributions or population change will also be influenced by other factors acting upon them either alone or in combination with climate (Simmons *et al.*, 2004; Sanderson *et al.*, 2006; Jetz *et al.*, 2007).

Another confounding effect, which may change the projection of climatic change impacts on migrant birds, is that the models relate mean climate to species' distributions. Although the future climate is likely to change in terms of means and has done so (e.g. mean increase in temperature, decrease precipitation, etc.), it will also change in terms of frequency of severe weather anomalies (Easterling *et al.*, 2000; IPCC, 2001; IPCC, 2007). Severe 'bad weather' affects species dramatically. For instance, several warbler populations crashed after droughts in the Sahel (Peach *et al.*, 1991). Populations of *Sylvia communis*, *Phoenicurus phoenicurus* and *Riparia riparia* declined in the West African Sahel region in the late 1960s due to drought (Jones *et al.*, 1996) and declines in *Acrocephalus schoenobaenus* populations in Britain between 1960 and 1980 can be related to rainfall fluctuations in their West African non-breeding grounds (Peach *et al.*, 1991). Weather anomalies are likely to affect Africa most (IPCC, 2007) which means that the projected increased climatic suitability for many species may not result in range expansion in the future. The effect of increased extreme weather events on populations is unknown. However, it is likely that it will affect migrant birds' phenology and demography (Berthold, 2001; Hubalek, 2004; Stokke *et al.*, 2005) more than their underlying distribution.

4.3 The influence of migratory strategy on climate change impacts

4.3.1 Introduction

Migration is a means for species to escape harsh winters and make use of different locations when food abundance is plentiful. The trade-off is that migration is energy demanding and often dangerous. Climate change has the potential either to exacerbate this by increasing migration distance and reducing food abundance or to improve conditions for some migrants as areas closer to the breeding ground become suitable in the non-breeding season.

Species can be either entirely resident, partially migratory (where part of a population is migratory) or obligate migrants. These traits are genetically controlled (see Chapter 2). However, climate could affect species' migratory behaviour through natural selection or phenotypic plasticity. For instance, many *Sylvia atricapilla* have started to winter in Britain (Bearhop *et al.*, 2005). Furthermore many *Turdus merula* breeding in central Europe, that until the mid 19th century migrated to the Mediterranean, now remain on their breeding grounds throughout the year (Birkhead, 2008).

Migrants can be divided into short-distance or long-distance migrants. Berthold (2001, 2003) suggested that climate change would affect these groups differently. Seasonal variation in temperature is thought to have influenced the proportion of migratory and resident birds through a diffuse competitive relationship between these groups (Lemoine and Böhning-Gaese, 2003). Analyses of long term population trends at Lake Constance in central Europe showed that long-distance migrants declined whilst short distance and resident species increased (c.f. Lemoine and Böhning-Gaese, 2003). Lemoine and Böhning-Gaese (2003) showed that these long-term trends were related to an increase in warmer winters.

In Europe, many long-distance migrants are currently declining (Sanderson *et al.*, 2006). Populations of Afro-Palaearctic migrants fluctuate with precipitation on the Sahelian wintering grounds (Baillie and Peach, 1992). Lemoine and Böhning-Gaese (2003) argue that short-term fluctuations and long-term trends may not be caused by the same factors. Theoretically, long-distance migrants are likely to decrease under climatic change because they rely on spatially separated areas that are often bio-climatically different (e.g. Eurasia and Africa) and that are affected by different processes and drivers of change, such as agricultural intensification in Europe and desertification in Africa. In contrast, resident species (and short-distance migrants)

should increase in numbers as milder winters increase survival rates (Schaefer *et al.*, 2008). Berthold (2001) hypothesised that under climate change partial and short distance migrants should become increasingly resident.

The impacts of climate change on (resident) breeding birds have already been well investigated (Harrison *et al.*, 2003; Huntley *et al.*, 2006; Jetz *et al.*, 2007; Huntley *et al.*, 2008). If climatic change is likely to affect different types of migrant birds differently it is important to investigate what the potential impacts on these groups are and how they differ. In this section, I compare the impacts of climate change between species' groups and also investigated changes in migratory strategy. From the literature (those cited here and in Chapter 2), I identified three hypotheses to test:

1) Trans-Saharan migrants will fare worse under climate change, as current population declines suggest. I expect, therefore, to show low overlap, low range extent, large range shifts and large changes in migration distance for trans-Saharan migrants. I also expect some species to newly over-winter north of the Sahara.
2) Short-distance migrants will fare better than long-distance migrants. The results should show larger overlap, range extent and smaller range shifts than for other migratory groups. Migratory species richness changes and community reassembly should also favour short-distance migrants.
3) Short-distance and split strategy migrants (see below) will become increasingly resident. I expect the results to show an increase in the number of resident areas for short-distance and split strategy migrants as well as an increase in short-distance strategies.

4.3.2 Methods

Although in most of the literature, migrant species have been divided into either short- or long-distance migrants, some species have a dual strategy. The 229 migrant bird species modelled in this thesis were, therefore, separated into three categories depending on their non-breeding region: short-distance European and North African migrants (E), long-distance trans-Saharan migrants (T) and split strategy migrants (S), i.e. species with non-breeding ranges North and South of the Sahara Desert (20° N). These categories were assigned to species from their recorded extent of occurrence (digital appendix) and not based on their simulated distribution. For each species/category, the multi-model mean measures of future change were calculated (see previous sections). There are 49 E migrants, 107 S migrants and 73 T migrants.

Differences among groups of migrants

Differences among species' groups were sought by comparing degree of overlap between current and future range, relative range extent and range shift (for both breeding and non-breeding models) between groups. Logit-transformed relative range extent and arcsine square root overlap values were tested for normality. Normally distributed variables were tested with a one-way ANOVA with Bonferroni *post hoc* test if the Levene's test showed that the variance was homogenous. If one or both of these conditions were not met, then Kruskal-Wallis tests were performed with Mann-Whitney *post hoc* tests with Bonferroni correction ($\alpha = 0.0167$).

Polar plots depicting species' direction of range shift for each modelling method and GCM were created with the different groups separated. Mean angle of range shift was calculated for each group. Average distances of range shift values were tested for normality. A one-way ANOVA or a Kruskal-Wallis was performed with relevant *post hoc* tests.

Mean proportional change in species richness (N) of each group was compared with Kruskal-Wallis tests to investigate changes in the composition of species richness in an area. The proportion of species from each of the migratory groups in each grid cell was also calculated for the present and the future. Anomalies between present and future absolute numbers were calculated for each category and plotted on to the study area to investigate the spatial pattern of change.

Kruskal-Wallis tests were performed on proportion change in mean, minimum and maximum migration distance with Mann-Whitney *post hoc* tests with Bonferroni correction ($\alpha = 0.0167$) between migratory groups.

Changes in migration strategy

The number of species in each migratory category was calculated for each simulation. Mean GAM, CRS and the multi-model mean were also calculated. A chi-square test was performed using the current simulated values as expected frequencies. Simulated values were used rather than absolute values so that only future differences were taken into account rather than differences arising from creating a model. European migrants with modelled range south of the Sahara desert (usually in South Africa) in the present period were re-classified as E migrants in the future simulations so as not to bias the results. Changes in categories were examined in terms of groups of migrants and as individual species. Consistent changes (among models) in categories for certain species were examined.

Residency

The number of 'resident' cells, i.e. number of overlapping breeding and non-breeding cells, for each species was counted in both current and future simulations. The proportion of 'resident' cells for each species' range was also calculated for the present and the future. From these values, anomalies were calculated for each species for each future simulation as well as for the mean future simulations. The number of positive, negative and no change anomalies were counted for each migrant group. A Kruskall-Wallis test was performed to see if species' geography (through Biome categories – Fig. 3.5 and Table 3.15) affected which species were more or less likely to gain/lose resident cells. The proportion of resident cells was used instead of absolute number because it was thought that changes in proportion of resident cells in a species' range would give a better indication of whether a species was becoming 'more' or 'less' resident. Using absolute numbers of cells would be misleading because the change in absolute number of resident cells could also be due to increases or decreases in range size.

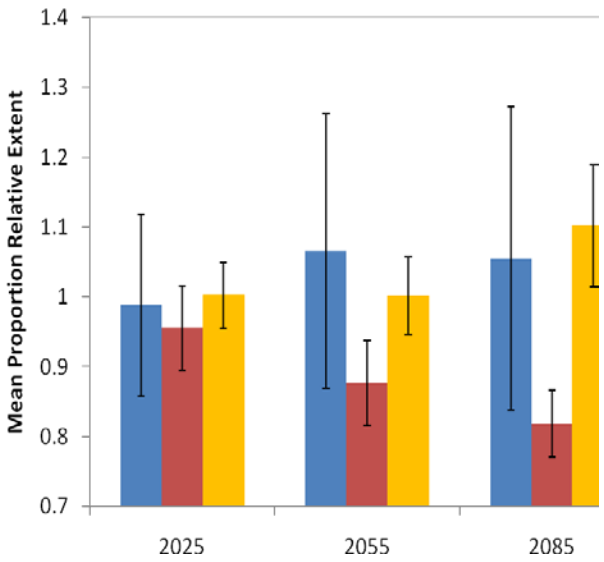
4.3.3 Results

Range extent

Figure 4.11 and Figure A5 show the multi-model mean relative extent for each category of species. The breeding range models exhibited some differences between the three groups (Fig. 4.11 a). There was greater variation among E migrants as can be seen from the larger error bars in Fig. 4.11a. For 2025, the groups differed in their range extent in the A1B scenario with European (E) migrants having a reduced range extent (0.908) compared to trans-Saharan (T) migrants (1.00) according to the *post hoc* tests ($U = 1239.5$, $p < 0.0167$); but not in the A2 scenario. For 2055, groups only differed in the A1B scenario. Post hoc tests showed that split strategy (S) migrants had significantly lower range extent than both E migrants ($U = 3107$, $p < 0.0167$) and T migrants ($U = 1324.5$, $p < 0.0167$). For 2085, groups exhibited differences for both A1B and A2 scenarios. Bonferroni *post hoc* tests showed that S migrants had significantly lower range extents than T migrants ($p < 0.01$). For both E and T migrants relative range extent increased through time, whereas range extent decreased for S species.

Migrant groups differed in their relative range extent for the non-breeding range models, though all groups increased in range (Fig. 4.11 b). For 2025, all groups were significantly different from each other. For 2055, groups also differed. Mann-Whitney *post hoc* tests showed that T migrants were significantly different from both E and S migrants (Fig. 4.11). In 2085, E migrants have significantly lower relative range extent than both S and T migrants. For both S and T migrants relative range extent increased through time, whereas relative range extent decreased for E species.

a



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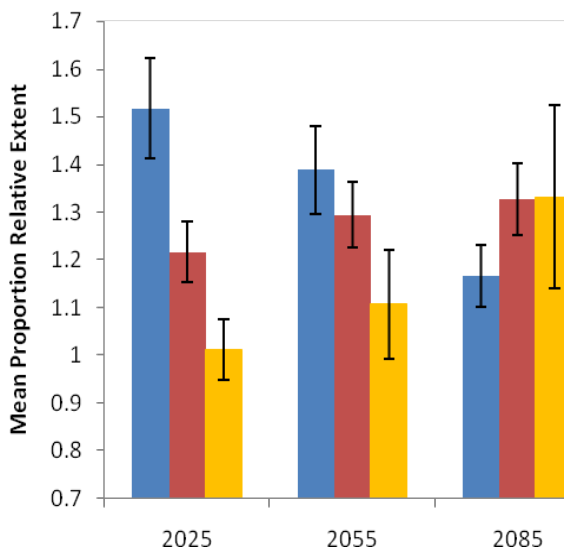
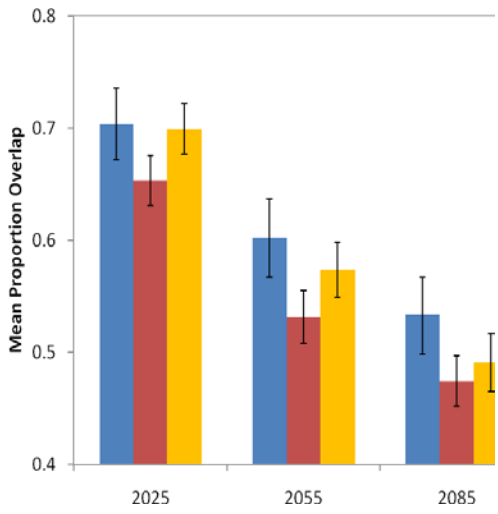


Figure 4.11: A1B Scenario multi-model mean relative extent for each category of species (blue: European, yellow: trans-Saharan and red: split strategy migrants); Error bars represent standard error across species. ANOVA or Kruskall Wallis tests for each time period are reported. a) breeding ground models (2025: $H_2 = 7.977$, $p < 0.05$; 2055: $H_2 = 8.594$, $p < 0.05$; 2085: $F_2 = 5.679$, $p < 0.01$); b) non-breeding ground models (2025:. $F_2 = 15.003$, $p < 0.001$; 2055: $H_2 = 23.382$, $p < 0.000$; 2085: $H_2 = 7.668$, $p < 0.05$)

Figure 4.12 and Figure A6 show the multi-model mean overlap for each category of species. On the breeding range, there was no difference in overlap between groups for all time periods and scenarios. Proportion overlap decreased through time.

On the non-breeding grounds, however, species' groups differed in their overlap between current and future range. Mann-Whitney *post hoc* tests show that in 2025 E and S had similar overlap (A1B: $U = 2372.5$, $p = 0.639$; A2: $U = 2174.5$, $p = 0.211$) but that E and T were different (A1B: $U = 1198$, $p < 0.001$; A2: $U = 1054.5$, $p < 0.001$) as were S and T (A1B: $U = 2937.5$, $p < 0.0167$; A2: $U = 2849.5$, $p < 0.0167$). Results were similar for 2055. In 2085, however, E and T migrants had similar overlap values (A1B: $U = 1427$, $p = 0.062$; A2: $U = 1447$, $p = 0.078$) while, E and S were different (A1B: $U = 1479$, $p < 0.001$; A2: $U = 1397$, $p < 0.001$) as were S and T (A1B: $U = 2337$, $p < 0.001$; A2: $U = 2309$, $p < 0.001$).

a



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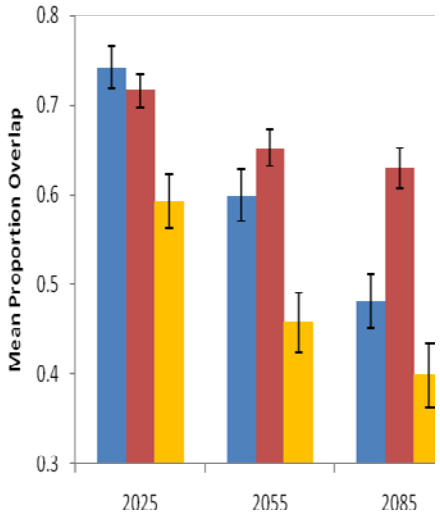
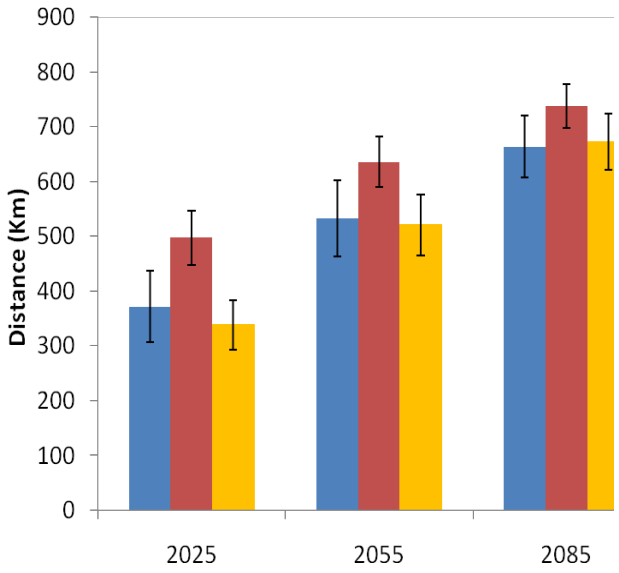


Figure 4.12: A1B Scenario multi-model mean proportion overlap for each category of species (blue: European, yellow: trans-Saharan and red: split strategy migrants); Error bars represent standard error across species. ANOVA or Kruskall Wallis tests for each time period are reported. a) breeding ground models (2025: F_2 =1.432, p = 0.241; 2055: F_2 =1.642, p = 0.196; 2085: F_2 = 0.845, p = 0.431); b) non-breeding ground models (2025: H_2 =12.896, p < 0.01;. 2055: H_2 =20.635, p < 0.001; 2085: H_2 = 30.369, p < 0.001).

Range shift

Figure 4.13 and Figure A7 show the multi-model mean average distance between current and future centroids. Shift of centroid on the breeding grounds did not differ significantly between migrant groups. There were some differences on the non-breeding grounds, however. Mann-Whitney *post hoc* tests showed that T migrants had significantly larger distances of shift in 2055 under the A1B scenario (U = 3105, p < 0.01) than S migrants. In 2085 A1B and A2 scenario, T migrants had significantly larger distances of shift than E or S migrants (A1B: U_{S-T} = 2429.5, p < 0.001; U_{E-T} = 1211, p < 0.01; A2: U_{S-T} = 2346, p < 0.001; U_{E-T} = 1183, p < 0. 01).

a



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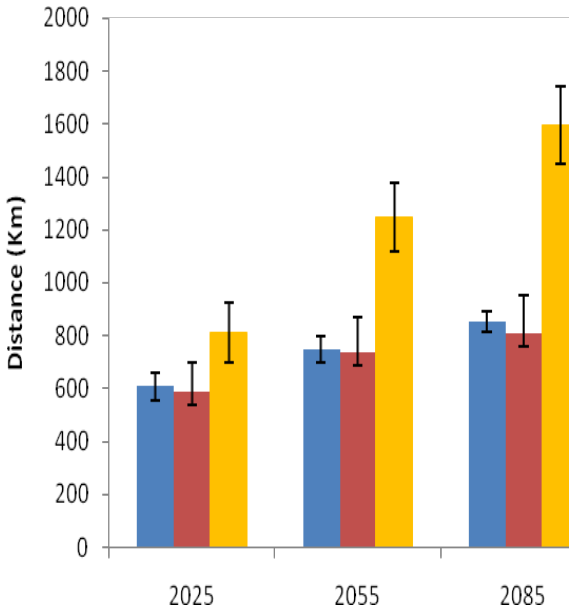


Figure 4.13: A1B Scenario multi-model mean average distance of range shift for each category of species (blue: European, yellow: trans-Saharan and red: split strategy migrants); a) breeding ground models, b) non-breeding ground models. Error bars represent standard error across species.

Figures 4.14-4.19 depict the angle of shift for each species' category on the breeding and non-breeding models under the A1B scenario. The A2 scenario can be found in Appendix III c. The polar plots also include arrows showing the mean direction of shift for each category. On the breeding grounds, the mean angle of shift of species' ranges is similar between categories; whereas on the non-breeding grounds, they are sometimes very different. The mean angles are slightly misleading as there is much spread between species. In general, species' ranges move mainly North on the European breeding grounds and North to East on the non-breeding grounds. The majority of European-wintering species' ranges move North-East (30°). For S species, the mean angle varies from 1° to 45° with quite a lot of spread. T migrants' mean angles vary across model projections. This shows that there are greater differences in prediction on the African non-breeding grounds between models.

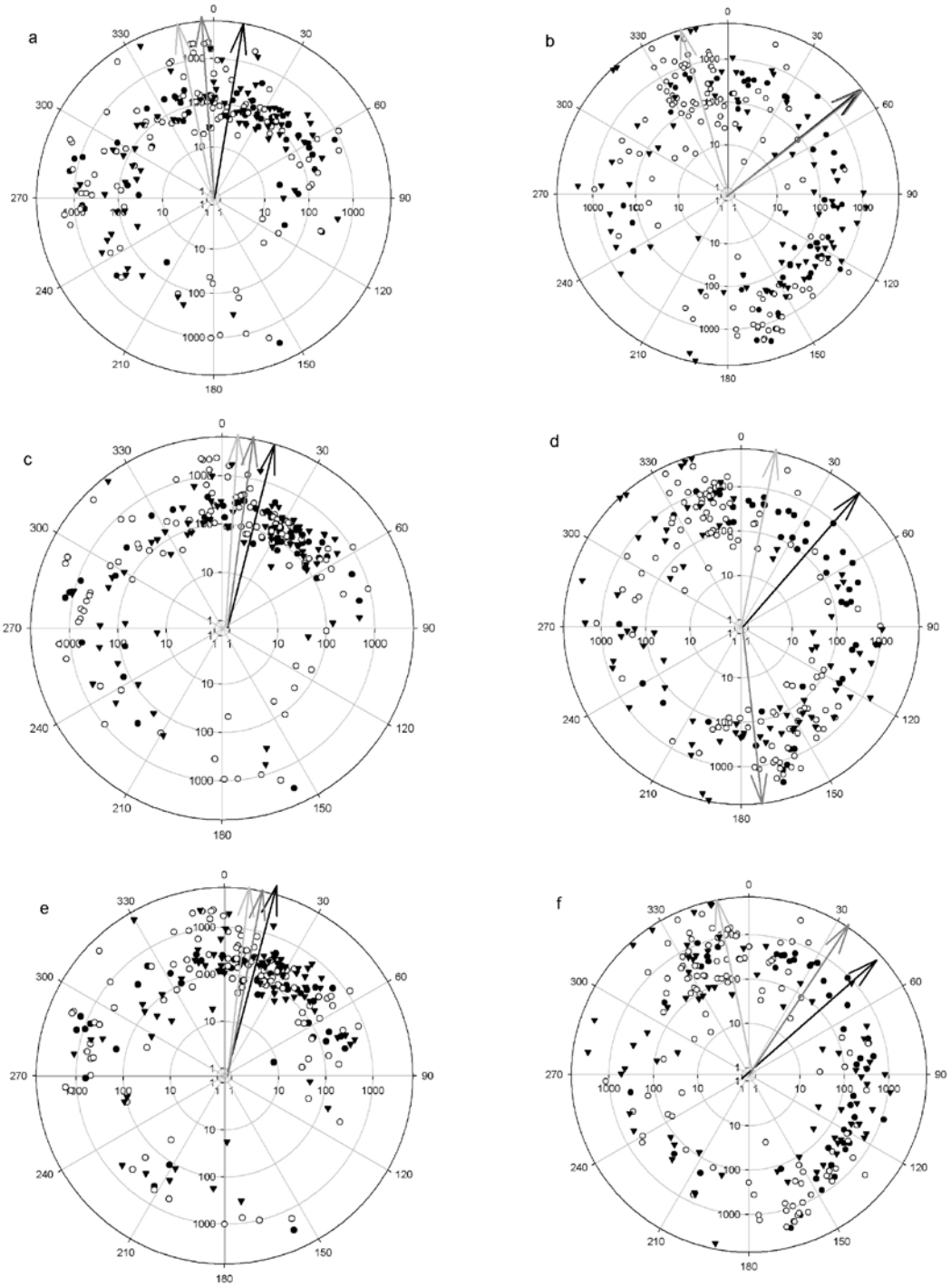


Figure 4.14: Direction of shift of species' ranges from GAM 2025 A1B scenario; a) Echam5 breeding, b) Echam5 non-breeding, c) GFDL breeding, d) GFDL non-breeding, e) HadGEM breeding, f) HadGEM non-breeding. Polar plots plotted on a log-scale with 7000km as the edge. Filled circles represent species with a European winter range and black arrow is the mean direction of shift; open circles represent species with a split non-breeding range and light grey arrow is the mean direction of shift; triangles represent species with a trans-Saharan non-breeding range and grey arrow is mean direction of shift.

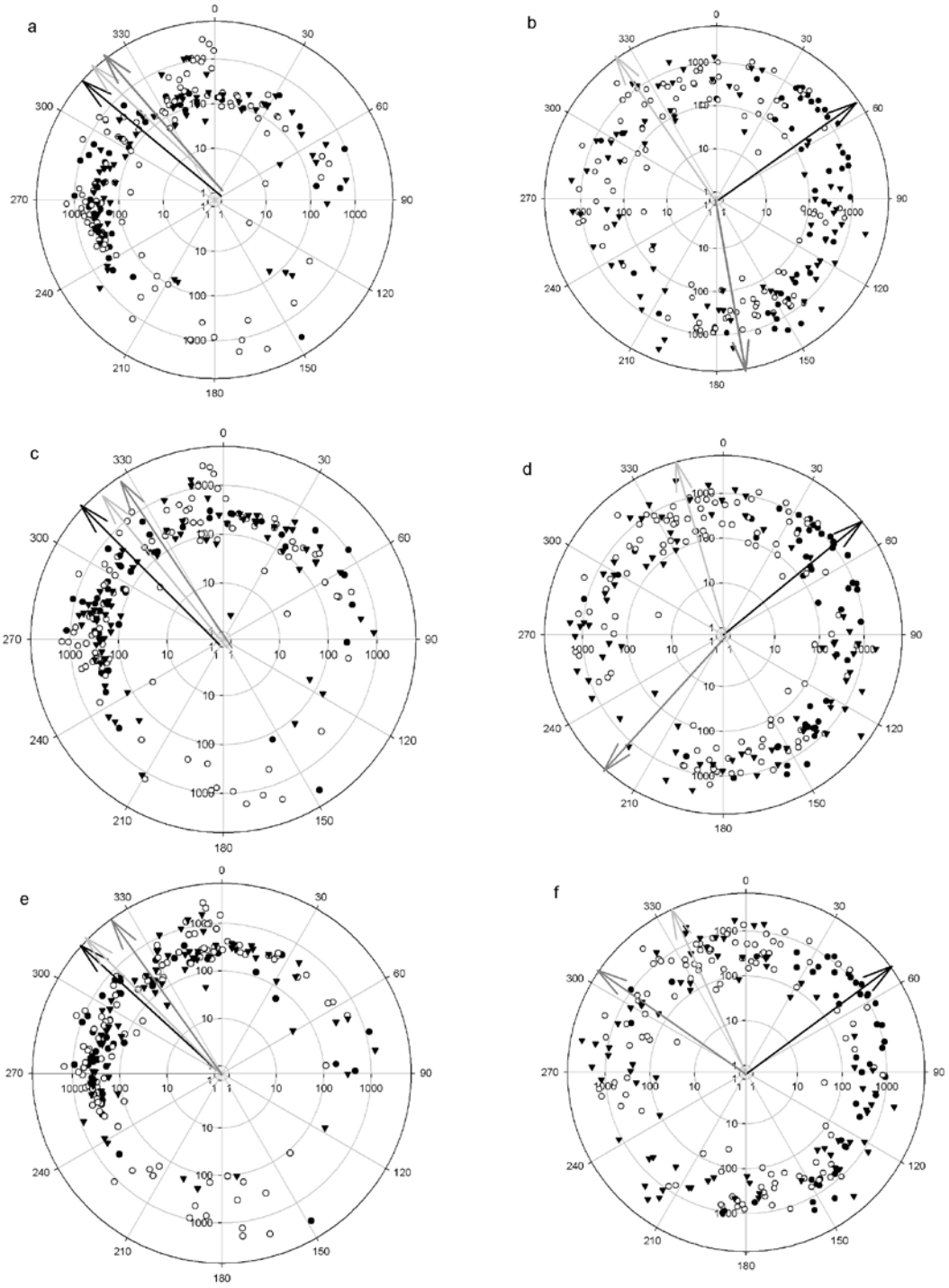


Figure 4.15: Direction of shift of species' ranges from CRS 2025 A1B scenario; a) Echam5 breeding, b) Echam5 non-breeding, c) GFDL breeding, d) GFDL non-breeding, e) HadGEM breeding, f) HadGEM non-breeding. Polar plots plotted on a log-scale with 7000km as the edge. Filled circles represent species with a European winter range and black arrow is the mean direction of shift; open circles represent species with a split non-breeding range and light grey arrow is the mean direction of shift; triangles represent species with a trans-Saharan non-breeding range and grey arrow is mean direction of shift.

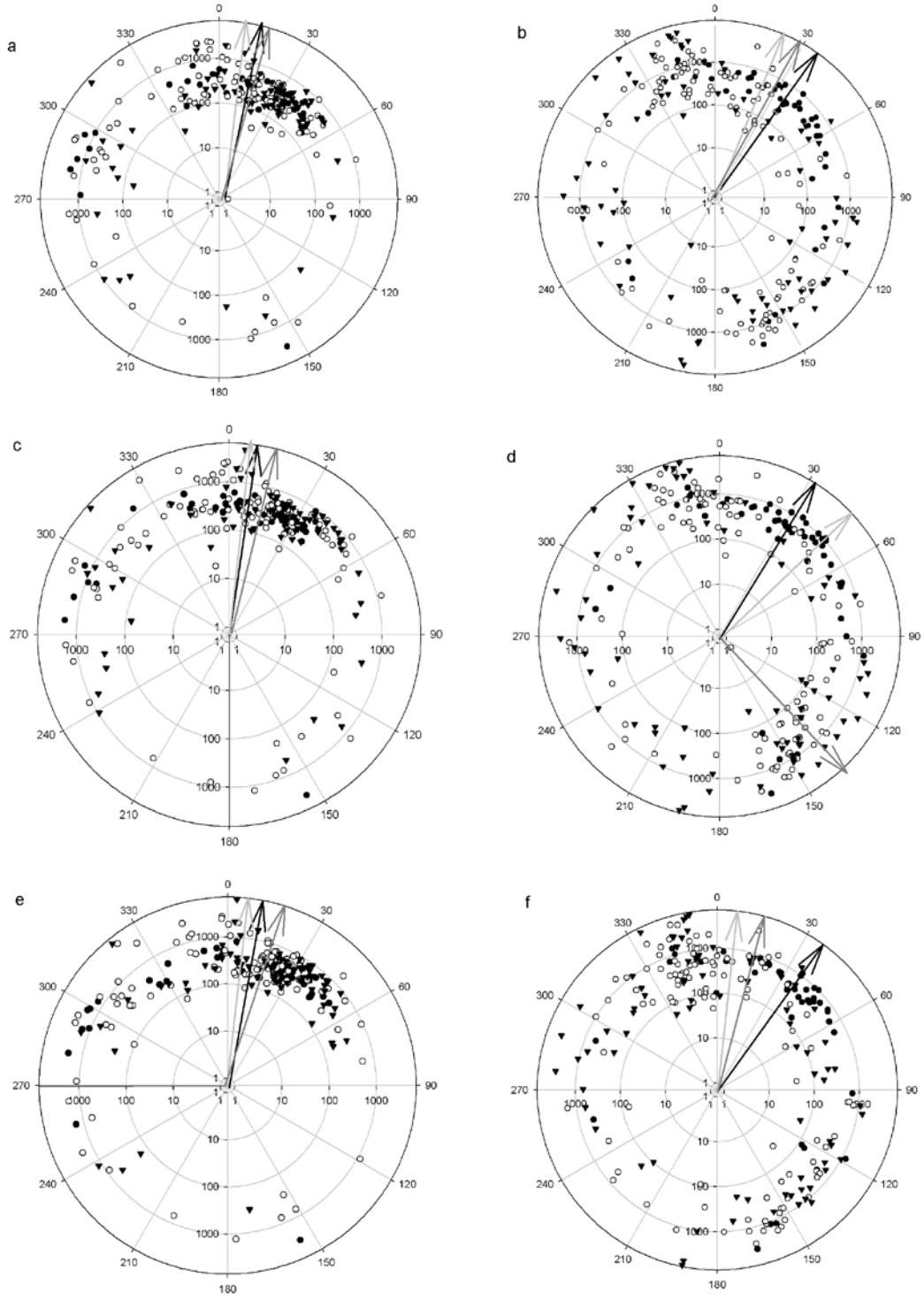


Figure 4.16: Direction of shift of species' ranges from GAM 2055 A1B scenario; a) Echam5 breeding, b) Echam5 non-breeding, c) GFDL breeding, d) GFDL non-breeding, e) HadGEM breeding, f) HadGEM non-breeding. Polar plots plotted on a log-scale with 7000km as the edge. Filled circles represent species with a European winter range and black arrow is the mean direction of shift; open circles represent species with a split non-breeding range and light grey arrow is the mean direction of shift; triangles represent species with a trans-Saharan non-breeding range and grey arrow is mean direction of shift.

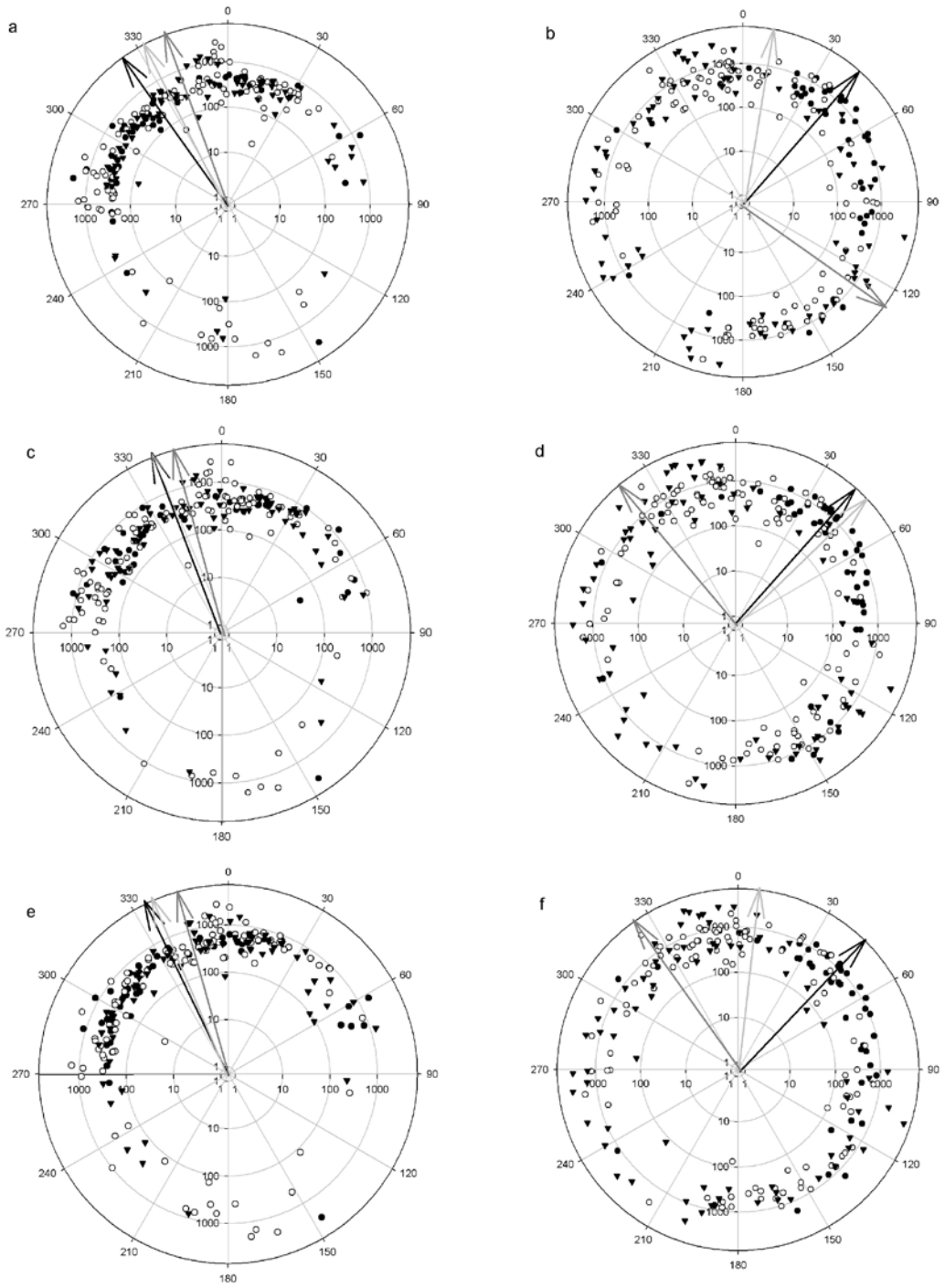


Figure 4.17: Direction of shift of species' ranges from CRS 2055 A1B scenario; a) Echam5 breeding, b) Echam5 non-breeding, c) GFDL breeding, d) GFDL non-breeding, e) HadGEM breeding, f) HadGEM non-breeding. Polar plots plotted on a log-scale with 7000km as the edge. Filled circles represent species with a European winter range and black arrow is the mean direction of shift; open circles represent species with a split non-breeding range and light grey arrow is the mean direction of shift; triangles represent species with a trans-Saharan non-breeding range and grey arrow is mean direction of shift.

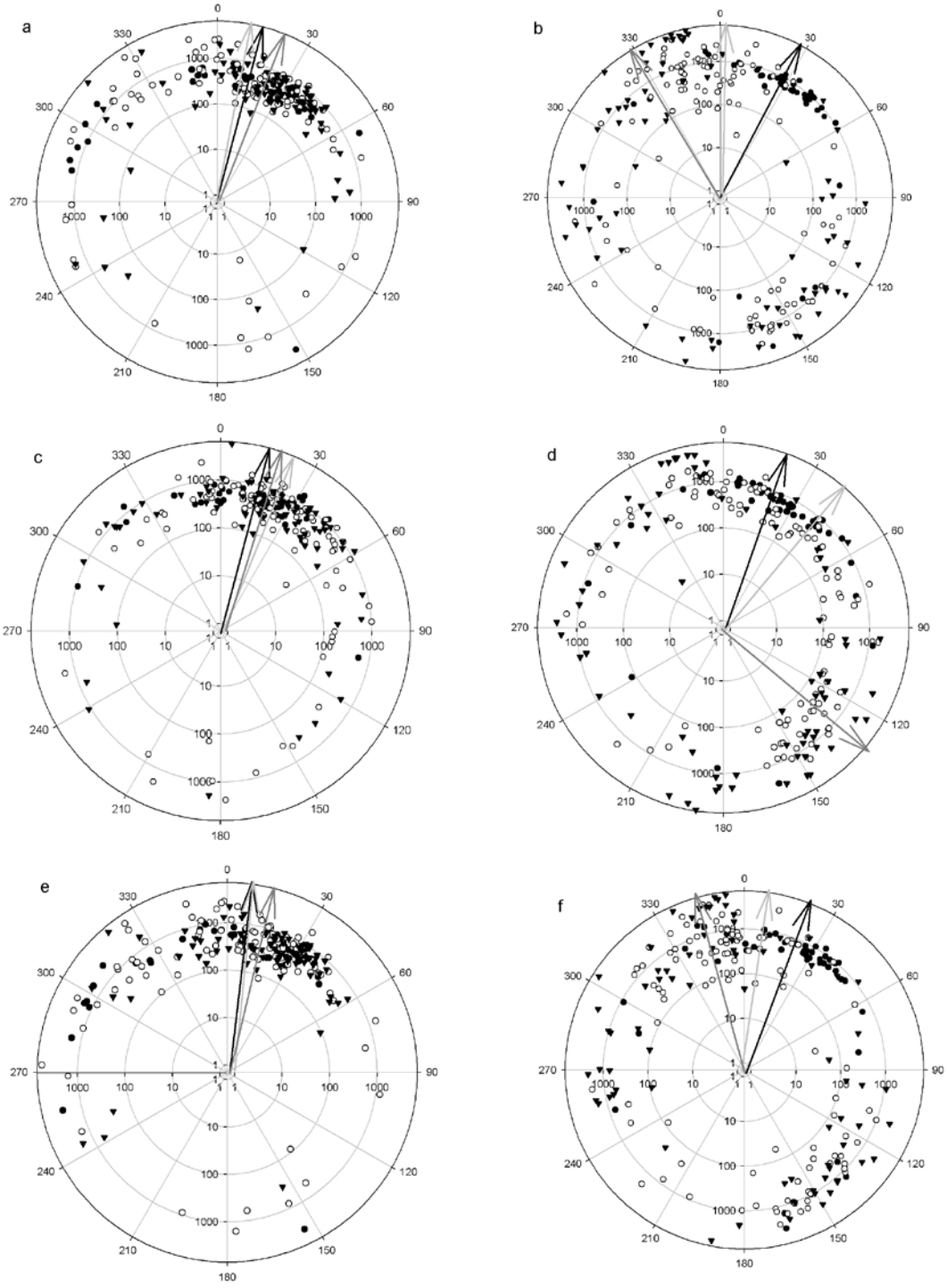


Figure 4.18: Direction of shift of species' ranges from GAM 2085 A1B scenario; a) Echam5 breeding, b) Echam5 non-breeding, c) GFDL breeding, d) GFDL non-breeding, e) HadGEM breeding, f) HadGEM non-breeding. Polar plots plotted on a log-scale with 7000km as the edge. Filled circles represent species with a European winter range and black arrow is the mean direction of shift; open circles represent species with a split non-breeding range and light grey arrow is the mean direction of shift; triangles represent species with a trans-Saharan non-breeding range and grey arrow is mean direction of shift.

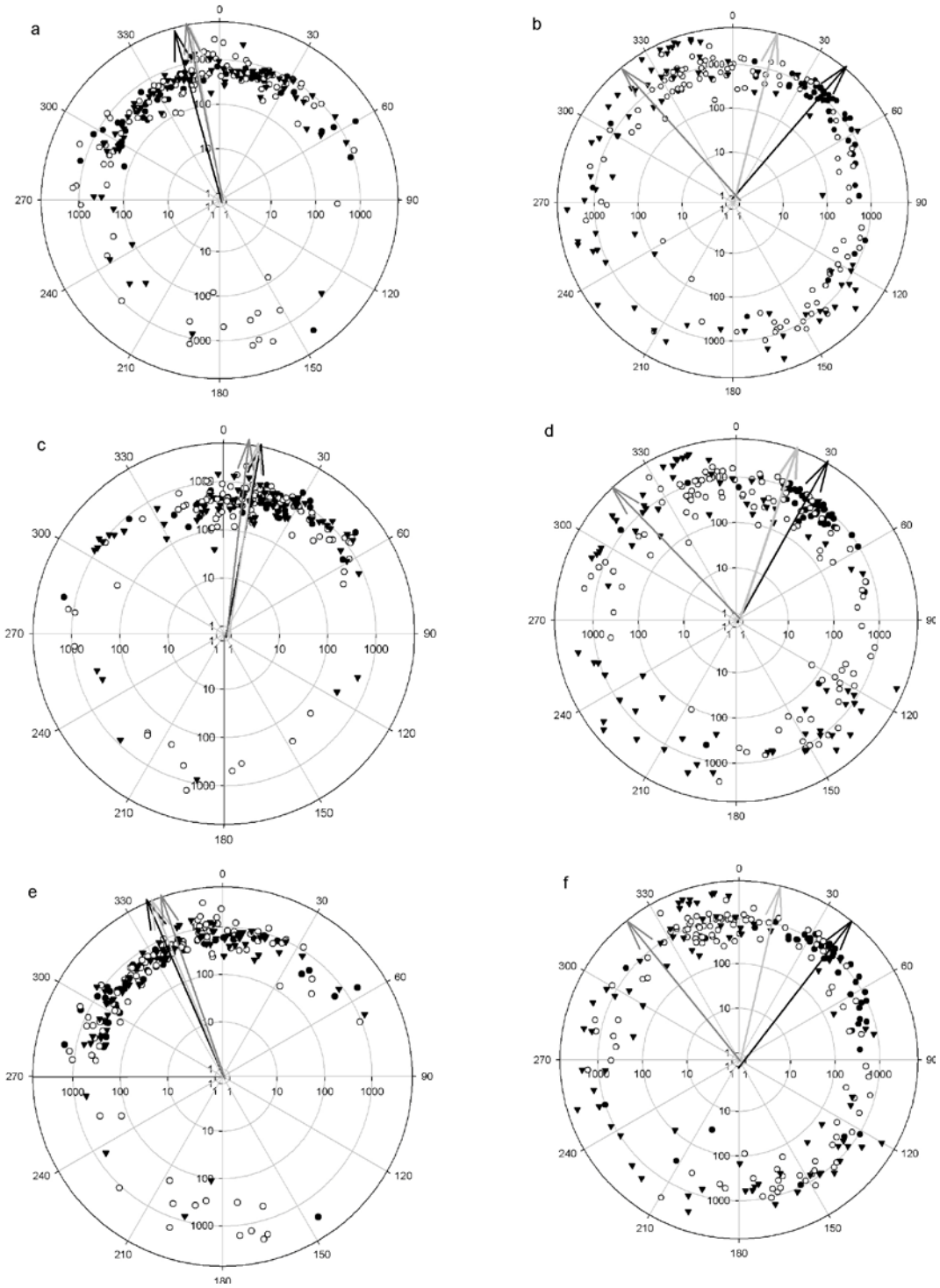


Figure 4.19: Direction of shift of species' ranges from CRS 2085 A1B scenario; a) Echam5 breeding, b) Echam5 non-breeding, c) GFDL breeding, d) GFDL non-breeding, e) HadGEM breeding, f) HadGEM non-breeding. Polar plots plotted on a log-scale with 7000km as the edge. Filled circles represent species with a European winter range and black arrow is the mean direction of shift; open circles represent species with a split non-breeding range and light grey arrow is the mean direction of shift; triangles represent species with a trans-Saharan non-breeding range and grey arrow is mean direction of shift.

Species richness

Under the A1B scenario in 2025, all groups displayed a significantly different change in species richness (Fig. 4.20); except between E and T species under the no dispersal projection on the non-breeding range (U = 5266000, p = 0.223). In 2055, all groups displayed a significantly different change in species richness; except between S and T species under the no dispersal projection on the breeding range (U = 52889747, p = 0.486). In 2085, however, there were some similarities between groups. S migrants showed similar change in species richness to E and T migrants on the breeding grounds assuming full dispersal (U = 52528325, p = 0.122 and U = 52552808, p = 0.141 respectively), and E and T migrants also had a similar change in species richness on the non-breeding grounds assuming full dispersal (U = 53097262, p = 0.844). Figure 4.20 illustrates these findings by depicting the average proportional change in species richness per cell under full and no dispersal for both breeding and non-breeding areas. All statistics and figures for the A2 scenario are in Figure A8 and are similar to the AIB scenario results.

a b

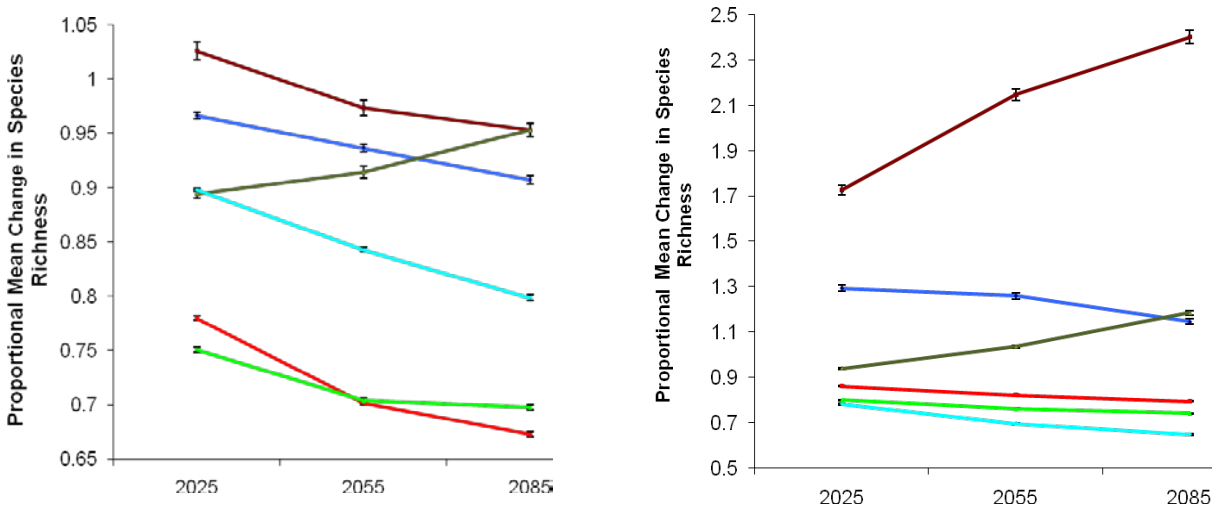


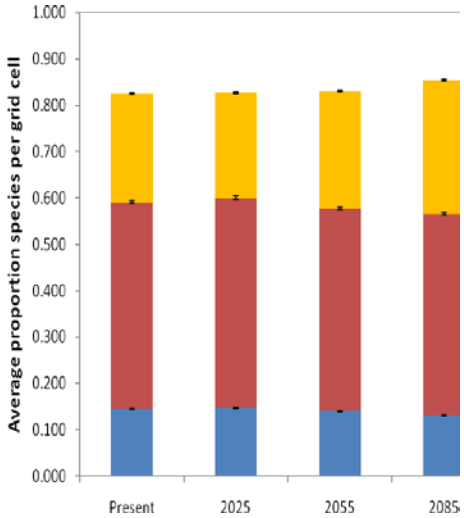
Figure 4.20: Relative change under the A1B scenario in species richness across cells for each category of species (Europe: blue, trans-Saharan: green, split strategy: red) under full dispersal (N; darker colours) and dispersal failure (No; lighter colours); Error bars represent standard error. Results of Kruskall Wallis test for each time period are also reported; a) breeding grounds (2025: N, H_2 = 184.7, $p < 0.001$; No, H_2 = 3399.9, $p < 0.001$; 2055: N, H_2 = 110.1, $p < 0.001$, No, H_2 = 2804.1, $p < 0.001$; 2085: N: H_2 =12.2, $p < 0.01$; No, H_2 =1951.3, $p < 0.001$); b) non-breeding grounds (2025: N, H_2 = 2424.5, $p < 0.001$; No, H_2 = 164.2, $p < 0.001$; 2055: N,H_2 = 2959.8, $p < 0.001$, No,: H_2 = 422.4, $p < 0.001$; 2085: N: H_2 =3400.6, $p < 0.001$; No, H_2 =632.6, $p < 0.001$).

On the breeding grounds (Fig. 4.20 a), the models projected that all groups were likely to lose numbers of species per grid cell relative to the current species richness. S migrants were predicted to have a greater number of species per grid cell than in the present in 2025 but gradually decreasing in numbers per grid cell over time. E migrants were also simulated to decrease in number over time. T migrants, on the other hand, are predicted to increase in number over time, although had a lower proportion of species relative to the present than other groups in 2025 and 2055. Assuming dispersal failure, all groups lost numbers of species in Europe, with S and T migrants losing more so than E migrants.

On the non-breeding grounds, grid cells gained S and T migrants, with S species increasing more than the other two groups through time. Grid cells were predicted to lose E species through time. Assuming dispersal failure, all groups have reduced numbers of species per grid cell relative to the present.

Figure 4.21 shows that on the breeding grounds, under full dispersal, T migrants increased in proportion to E and S migrants on average for the A1B Scenario (A2 Scenario in Fig. A9). On the non-breeding grounds, whilst proportions stayed very similar, under both dispersal scenarios, S migrants' proportion increased on average in detriment to E migrant species. T migrants' proportion stayed very similar. The proportion change under the no dispersal scenario is virtually the same as under the full dispersal scenario.

a



b

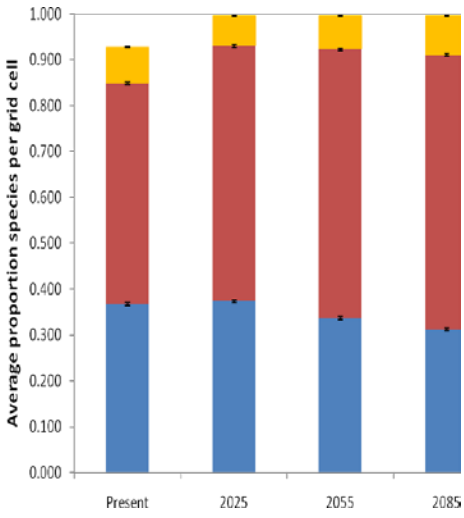


Figure 4.21: Multi-model average proportion in each grid cell of European, split strategy and trans-Saharan migrants in the present and future A1B scenario; a) breeding grounds, b) non-breeding grounds. Blue = European migrants, Yellow = trans-Saharan migrants and Red = split-strategy migrants.

Figures 4.22-4.24 depict community reassembly in different parts of the range for the three time slices for the A1B scenario. Figures A10-A12 show the same for the A2 scenario. On the breeding range, split strategy migrants decreased in numbers throughout Europe whilst trans-Saharan migrants increased in northern Europe. European migrants decreased in southern Europe and increased in northern Europe. On the European winter grounds, European migrants increased in northern Europe. On the African winter quarters, split strategy migrants gained territory as trans-Saharan migrants lost ground.

Changes in the proportion of migrants in each grid cell can be found in the digital appendix and further depict community reassembly. However, because change is reported as proportional, increases or decreases for only one species in areas where it was not found before, results in inflated anomalies. On the breeding range, the proportion of split strategy migrants decreased in the North and increased in the South in opposition to trans-Saharan migrants. The proportion of European migrants decreased in southern Europe and increased in central Europe. On the European winter grounds, the proportion of European migrants increased in Scandinavia but decreased in most areas. On the African winter quarters, the proportional change in migrants is the same as the change in absolute numbers.

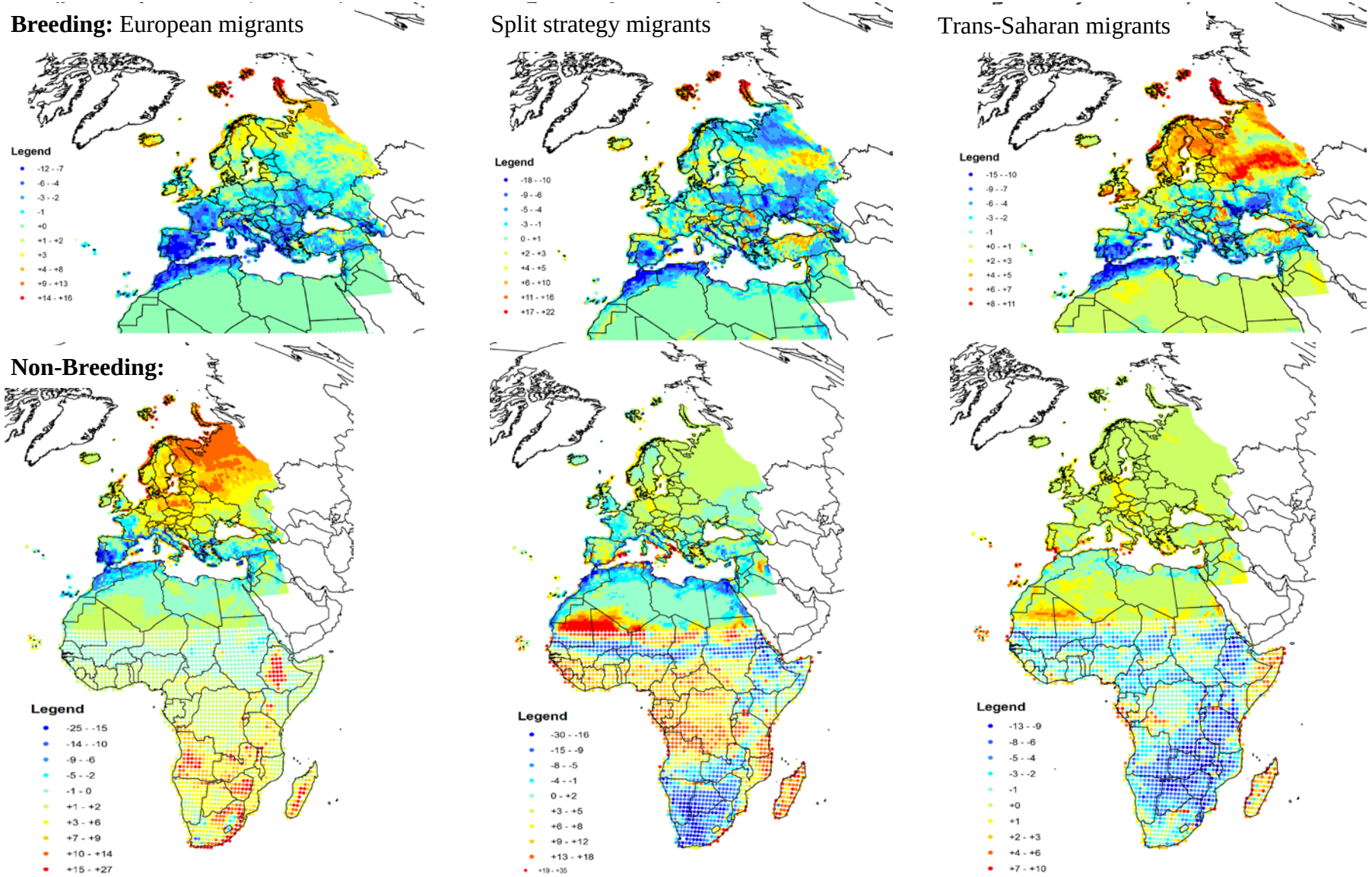


Figure 4.22: Anomalies between current and future numbers of species per grid cell for the 2025 A1B scenario for each category of migrants (European, split strategy, trans-Saharan). Blue colours depict reduced number of species, whilst yellow and red represent gains.

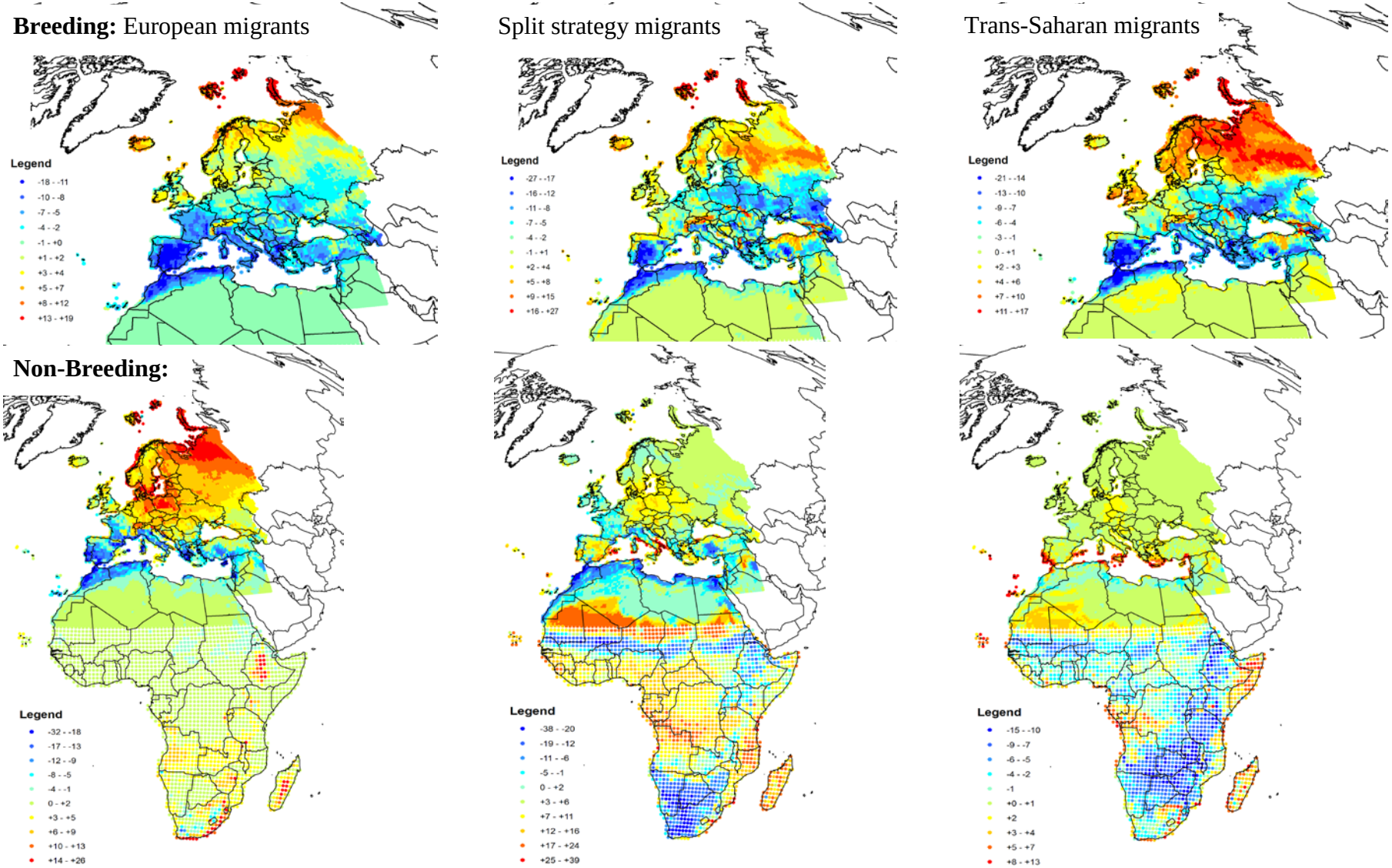


Figure 4.23: Anomalies between current and future numbers of species per grid cell for the 2055 A1B scenario for each category of migrants (European, split strategy, trans-Saharan). Blue colours depict reduced number of species, whilst yellow and red represent gains.

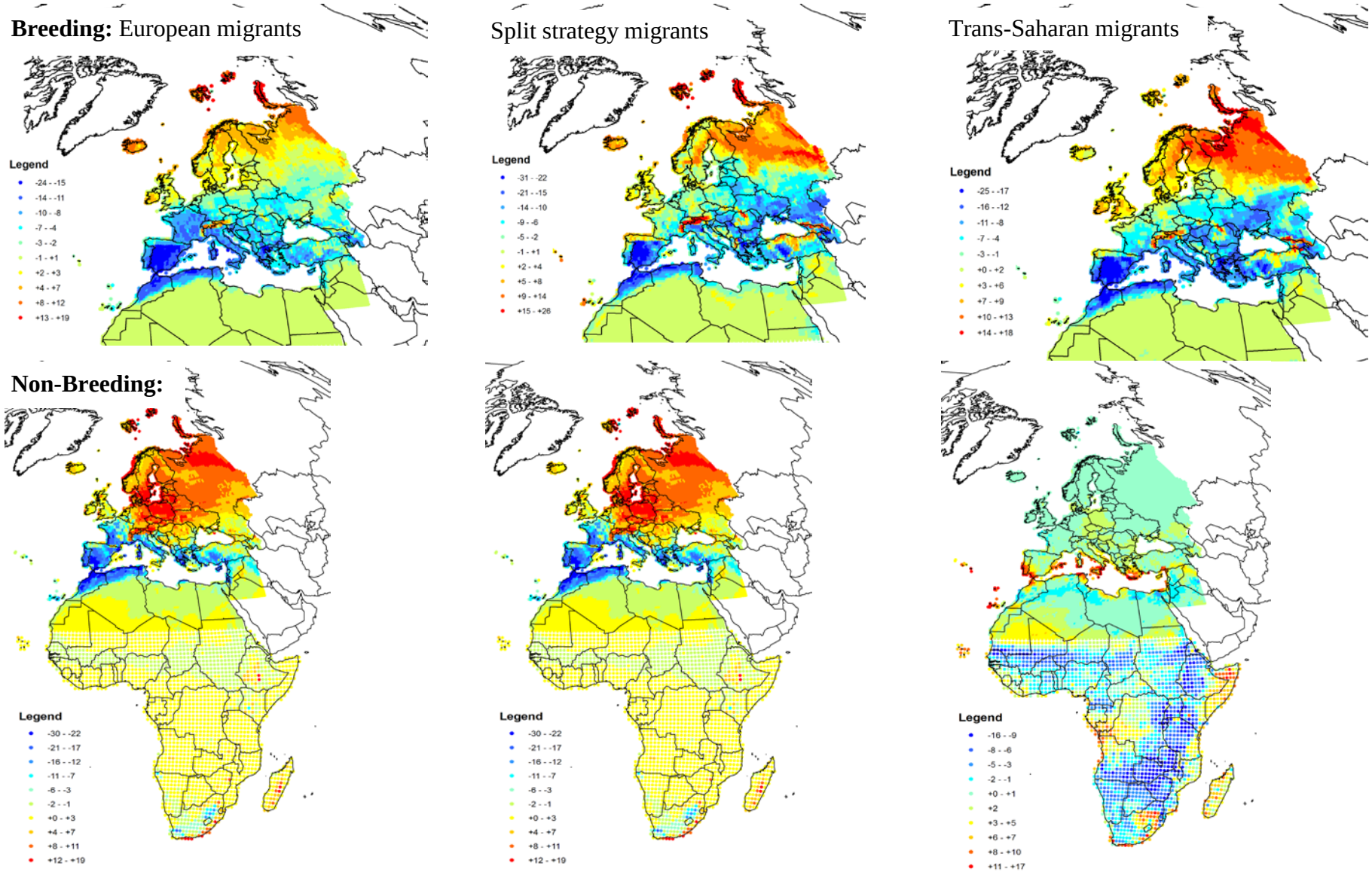


Figure 4.24: Anomalies between current and future numbers of species per grid cell for the 2085 A1B scenario for each category of migrants (European, split strategy, trans-Saharan). Blue colours depict reduced number of species, whilst yellow and red represent gains.

Migration distance

On average, mean migration distances increased under future climate change scenarios (Tables 4.20-4.22). However, some species are projected to have smaller distances to travel in the future. Kruskal-Wallis tests on proportional mean migration distance showed that there was no significant difference between migratory groups (Table A14).

In general, future maximum migration distances were projected to be similar to current figures with a multi-model median proportional change of 1.018 for all species and range 0.968-1.121. For 2025 A2 and 2055 A2, there was also no significant difference between the three migrant groups in terms of proportional changes in maximum distances (Table A15). However, for 2025 A1B and 2055 A1B, change in maximum distances was different with T migrants having a greater increase in distance than S migrants (2025 A1B: $U = 2883$, $p < 0.01$; 2055 A1B: $U = 2405$, $p < 0.001$) but not E migrants (medians: E = 1.022, S = 1.012, T = 1.023 for 2025 A1B; E = 1.037, S = 1.023, T = 1.058 for 2055 A1B). Under 2085 predicted climatic change, proportional change in maximum migration distances was different between migrant groups, with E migrants showing no change in distance in the A1B scenario (median proportional change: 1.02) or a decrease in the A2 scenario (median of 0.952). Trans-Saharan migrants were simulated to have greater increases (median of 1.06 and 1.07 for A1B and A2 respectively) in maximum distances than the other migrants.

There was more variation of change in minimum distances among species with some species gaining 'resident' climate space, i.e. having overlapping breeding and non-breeding grid cells, thereby effectively decreasing minimum migration distance to zero, and other species' minimum migration distance increasing by 100%. For 2025, there was no difference between migrants' change in minimum migration distance (Table A16). In 2055, there was a difference under the A1B scenario ($H_2 = 7.146$, $p < 0.05$). The difference was only between E and T migrants ($U = 1214$, $p < 0.01$) with medians of 1 for E migrants and 0.89 for T migrants. In 2085, minimum distances were also different between migrants (A1B: $H_2 = 14.994$, $p \leq 0.001$; A2: $H_2 = 24.709$, $p < 0.000$). Under both scenarios, S and E migrants were no different (A1B: $U = 3294$, $p = 0.230$; A2: $U = 3325$, $p = 0.269$) while minimum migration distances decreased for T migrants.

Table 4.20: Migration distances for European, split strategy and trans-Saharan migrants for the present and 2025. Average migration distance (M), relative change in migration distance (Pm) and minimum and maximum migration distance in Km. 10^{th} and 90^{th} percentiles are also given (M_{10}-M_{90}).

				A1B emissions scenario						A2 emissions scenario					
		Present		GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
		GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
Europe	M	1347	1160	1506	1379	1534	1396	1542	1433	1425	1354	1501	1391	1515	1437
	M_{10}-M_{90}	294-2327	280-2060	325-2537	527-2592	351-2604	566-2624	327-2754	618-2619	222-2534	556-2464	328-2475	590-2562	416-2631	635-2644
	Pm	n/a	n/a	1.19	1.49	1.25	1.53	1.27	1.57	1.12	1.46	1.21	1.53	1.25	1.58
	Pm_{10}-Pm_{90}	n/a	n/a	0.48-1.85	0.67-3.03	0.51-1.81	0.65-3.15	0.56-1.99	0.72-3.29	0.38-1.65	0.67-2.97	0.48-1.72	0.68-3.08	0.52-1.94	0.72-3.24
	Mmin	53	43	138	53	101	42	115	48	115	45	111	45	110	16
	$Mmin_{10}$-$Mmin_{90}$	0-60	0-83	0-464	0-61	0-135	0-50	0-123	0-59	0-107	0-49	0-243	0-62	0-157	0-50
	Mmax	8569	8740	8383	9164	8618	9152	8413	9154	8305	9151	8630	8496	8547	9173
	$Mmax_{10}$-$Mmax_{90}$	7157-9748	7974-9613	5126-9955	8223-9975	7225-9949	8029-9962	5139-9978	8009-9966	4179-9954	8014-9963	7400-9943	7452-9528	6581-9968	8005-9965
Split	M	3407	3161	3680	3217	3662	3205	3662	3195	3681	3246	3626	3176	3652	3200
	M_{10}-M_{90}	1164-6206	836-6174	1021-6459	899-6006	1170-6380	831-6074	935-6436	865-6116	1008-6464	826-6051	1082-6437	815-6088	1082-6428	935-6048
	Pm	n/a	n/a	1.22	1.14	1.21	1.14	1.21	1.09	1.19	1.15	1.19	1.09	1.20	1.13
	Pm_{10}-Pm_{90}	n/a	n/a	0.67-1.63	0.84-1.45	0.67-1.66	0.81-1.36	0.73-1.71	0.79-1.40	0.69-1.64	0.83-1.41	0.65-1.64	0.80-1.34	0.69-1.68	0.81-1.43
	Mmin	478	316	499	169	458	229	429	189	449	206	469	250	466	217
	$Mmin_{10}$-$Mmin_{90}$	0-1405	0-1024	0-1750	0-595	0-1330	0-750	0-1251	0-718	0-1320	0-670	0-1389	0-808	0-1457	0-735
	Mmax	8880	8945	8805	9124	8769	9077	8805	9117	8772	9114	8768	8616	8809	9135
	$Mmax_{10}$-$Mmax_{90}$	7758-9960	7898-9960	7694-9977	8223-9975	7614-9960	8091-9967	7761-9972	8160-9972	7419-9975	8138-9977	7506-9960	7359-9511	7783-9974	8165-9970

Table 4.20 continued		Present		A1B emissions scenario						A2emissions scenario					
				GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
		GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
Trans	M	4496	4547	4839	4748	4702	4704	4726	4740	4786	4770	4660	4672	4729	4702
	M_{10}-M_{90}	2333-6456	1763-7350	2346-7124	2257-6678	2226-7137	2139-6809	2388-7045	2366-6791	2473-7061	2303-6791	2349-7030	2024-6781	2187-6987	2316-6779
	Pm	n/a	n/a	2.11	1.29	2.01	1.25	2.02	1.35	2.02	1.28	1.97	1.24	1.99	1.30
	Pm_{10}-Pm_{90}	n/a	n/a	0.77-1.35	0.88-1.35	0.72-1.25	0.90-1.27	0.72-1.29	0.90-1.34	0.77-1.39	0.89-1.39	0.72-1.25	0.90-1.32	0.70-1.24	0.90-1.32
	Mmin	2461	2300	2530	1895	2451	1873	2295	1781	2400	1978	2369	1946	2282	1736
	$Mmin_{10}$-$Mmin_{90}$	121-4377	25-3821	53-4461	0-3653	145-4346	0-3586	119-4391	0-3665	141-4223	24-3847	435-4242	130-3708	15-4382	0-3661
	Mmax	7705	7826	7652	8463	7559	8362	7602	8451	7639	8514	7580	8932	7570	8523
	$Mmax_{10}$-$Mmax_{90}$	5525-9496	5386-9483	4751-9444	6983-9614	4761-9483	6989-9582	4744-9453	6854-9606	4725-9494	7023-9575	4716-9418	7818-9785	5125-9539	6812-9636

Table 4.21: Migration distances for European, split strategy and trans-Saharan migrants for the present and 2055. Average migration distance (M), relative change in migration distance (Pm) and minimum and maximum migration distance in Km. 10^{th} and 90^{th} percentiles are also given (M_{10}-M_{90}).

		Present		A1B emissions scenario						A2 emissions scenario					
				GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
		GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
Europe	M	1347	1160	1376	1335	1405	1288	1446	1396	1305	1281	1350	1276	1433	1392
	M_{10}-M_{90}	294-2327	280-2060	236-2601	544-2698	240-2724	569-2513	281-2804	618-2828	217-2452	537-2572	226-2615	554-2547	297-2640	613-2592
	Pm	n/a	n/a	1.07	1.43	1.08	1.42	1.13	1.51	1.00	1.39	1.03	1.41	1.14	1.53
	Pm_{10}-Pm_{90}	n/a	n/a	0.39-1.68	0.67-2.78	0.47-1.80	0.55-3.03	0.49-1.82	0.69-3.05	0.42-1.52	0.57-2.86	0.38-1.62	0.51-2.98	0.54-1.76	0.68-3.00
	Mmin	53	43	151	45	119	42	115	50	144	37	137	41	127	42
	$Mmin_{10}$-$Mmin_{90}$	0-60	0-83	0-297	0-58	0-211	0-59	0-167	0-70	0-392	0-49	0-330	0-73	0-206	0-50
	Mmax	8569	8740	8314	9204	8370	9148	8314	9261	8302	9153	8470	9232	8531	9281
	$Mmax_{10}$-$Mmax_{90}$	7157-9748	7974-9613	3981-9961	8367-9958	4108-9962	8150-9955	4200-9957	8218-9962	3979-9939	8305-9734	5539-9946	8031-9954	5597-9978	8217-9971

		Present		A1B emissions scenario						A2 emissions scenario					
				GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
Table 4.21 continued		GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
Split	M	3407	3161	3780	3290	3702	3262	3753	3251	3686	3216	3650	3237	3721	3218
	M_{10}-M_{90}	1164-6206	836-6174	1034-6802	800-6207	1035-6442	930-6071	990-6560	762-6105	981-6643	743-6104	924-6443	887-6053	943-6442	732-6053
	Pm	n/a	n/a	1.27	1.20	1.24	1.19	1.28	1.11	1.23	1.15	1.21	1.15	1.26	1.10
	Pm_{10}-Pm_{90}	n/a	n/a	0.59-1.74	0.77-1.62	0.67-1.74	0.79-1.49	0.58-1.78	0.74-1.51	0.56-1.68	0.74-1.47	0.64-1.66	0.76-1.48	0.57-1.77	0.72-1.49
	Mmin	478	316	417	98	404	120	361	92	427	103	392	128	370	96
	$Mmin_{10}$-$Mmin_{90}$	0-1405	0-1024	0-1029	0-287	0-1150	0-400	0-1303	0-260	0-1205	0-305	0-1220	0-493	0-1185	0-334
	Mmax	8880	8945	8888	9235	8845	9200	8871	9196	8845	8731	8829	9191	8860	9223
	$Mmax_{10}$-$Mmax_{90}$	7758-9960	7898-9960	7794-9989	8271-9987	7755-9986	8088-9981	7786-9989	8091-9986	7637-9988	7660-9680	7739-9985	8063-9984	7782-9989	8195-9987
Trans	M	4496	4547	5037	4785	4827	4797	4875	4820	44983	4830	4829	4754	4873	4829
	M_{10}-M_{90}	2333-6456	1763-7350	2513-7083	2448-6441	2210-6885	2363-6525	2497-6906	2492-6696	2506-6976	2350-6512	2423-6925	2370-6569	2619-6921	2574-6586
	Pm	n/a	n/a	2.26	1.35	2.19	1.33	2.20	1.36	2.26	1.36	2.13	1.31	2.20	1.34
	Pm_{10}-Pm_{90}	n/a	n/a	0.71-1.68	0.76-1.56	0.68-1.57	0.74-1.62	0.75-1.50	0.78-1.63	0.74-1.59	0.83-1.62	0.72-1.42	0.73-1.46	0.75-1.46	0.79-1.46
	Mmin	2461	2300	2408	1741	2284	1630	2278	1417	2370	1835	2311	1598	2184	1332
	$Mmin_{10}$-$Mmin_{90}$	121-4377	25-3821	0-4586	0-3995	0-4381	0-3762	0-4415	0-3447	0-4490	0-4045	0-4390	0-3807	0-4198	0-3285
	Mmax	7705	7826	7840	8683	7889	8621	7898	8680	7822	9309	7855	8555	7929	8804
	$Mmax_{10}$-$Mmax_{90}$	5525-9496	5386-9483	4502-9649	7284-9798	4890-9537	7057-9748	5543-9583	7149-9802	4427-9580	8521-9904	4965-9578	6838-9727	5450-9718	7169-9862

Table 4.22: Migration distances for European, split strategy and trans-Saharan migrants for the present and 2085. Average migration distance (M), relative change in migration distance (Pm) and minimum and maximum migration distance in Km.. 10^{th} and 90^{th} percentiles are also given (M_{10}-$M_{90)}$.

				A1B emissions scenario						A2 emissions scenario					
		Present		GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
		GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
Europe	M	1347	1160	1244	1039	1355	1261	1491	1278	1187	1061	1369	1265	1561	1334
	M_{10}-M_{90}	294-2327	280-2060	347-2071	324-1790	193-2927	528-2539	207-2981	591-2274	293-2125	342-1782	215-3116	559-2458	214-3394	654-2399
	Pm	n/a	n/a	1.02	0.99	1.03	1.41	1.16	1.45	0.99	0.97	1.03	1.43	1.25	1.49
	Pm_{10}-Pm_{90}	n/a	n/a	0.67-1.32	0.47-1.72	0.46-1.68	0.56-3.21	0.51-1.96	0.62-2.99	0.51-1.43	0.36-1.53	0.43-1.82	0.56-3.16	0.45-2.16	0.59-3.09
	Mmin	53	43	118	12	140	49	158	43	140	14	161	32	163	42
	$Mmin_{10}$-$Mmin_{90}$	0-60	0-83	0-158	0-21	0-179	0-115	0-407	0-71	0-252	0-45	0-294	0-58	0-544	0-49
	Mmax	8569	8740	7221	8523	8234	9201	8326	9219	5959	8588	8723	9243	8296	9299
	$Mmax_{10}$-$Mmax_{90}$	7157-9748	7974-9613	3480-9345	5983-9743	3644-9956	8318-9952	3947-9966	8290-9963	3175-9261	6352-9806	7370-9968	8334-9956	4397-9965	8322-9956
Split	M	3407	3161	3606	3360	3762	3229	3836	3242	3563	3390	3750	3207	3815	3173
	M_{10}-M_{90}	1164-6206	836-6174	923-6651	847-6610	948-6714	768-6134	991-6687	794-6097	951-6689	818-6672	879-6652	781-6121	989-6572	737-6112
	Pm	n/a	n/a	1.14	1.18	1.32	1.17	1.34	1.20	1.15	1.07	1.31	1.17	1.39	1.18
	Pm_{10}-Pm_{90}	n/a	n/a	0.79-1.34	0.75-1.49	0.63-1.86	0.70-1.62	0.63-1.93	0.67-1.63	0.73-1.38	0.63-1.29	0.65-1.87	0.72-1.59	0.59-1.95	0.64-1.68
	Mmin	478	316	338	68	358	72	350	70	274	68	338	72	339	59
	$Mmin_{10}$-$Mmin_{90}$	0-1405	0-1024	0-929	0-170	0-957	0-211	0-1246	0-193	0-910	0-163	0-916	0-173	0-1198	0-112
	Mmax	8880	8945	9015	9324	8823	9263	8884	9296	8986	9304	8306	9270	8882	9313
	$Mmax_{10}$-$Mmax_{90}$	7758-9960	7898-9960	7917-9991	8310-9994	7766-9989	8159-9988	7785-9989	8243-9988	7912-9993	8292-9995	4503-9970	8198-9989	7659-9990	8277-9992

		Present		A1B emissions scenario						A2 emissions scenario					
				GFDL		ECHAM		HadGEM		GFDL		ECHAM		HadGEM	
Table 4.22 continued		GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
Trans	M	4496	4547	5067	4923	4921	4578	4944	4767	4851	4922	5063	4581	4946	4710
	M_{10}-M_{90}	2333-6456	1763-7350	2545-6763	2356-6843	2396-7046	2165-6461	2682-7038	2447-6682	2135-6822	2229-6936	2407-7200	2087-6369	2187-7014	2404-6634
	Pm	n/a	n/a	1.21	1.23	2.28	1.30	2.25	1.37	1.15	1.17	2.29	1.29	2.25	1.38
	Pm_{10}-Pm_{90}	n/a	n/a	0.79-1.86	0.68-1.75	0.57-1.85	0.53-1.77	0.69-1.74	0.69-1.61	0.68-1.74	0.66-1.54	0.57-2.08	0.55-1.53	0.68-1.78	0.61-1.55
	Mmin	2461	2300	2346	1440	1978	1238	2029	1158	1978	1280	2188	1428	1965	1127
	$Mmin_{10}$-$Mmin_{90}$	121-4377	25-3821	0-4676	0-4073	0-4395	0-3460	0-4247	0-3130	0-4442	0-3959	0-5180	0-3982	0-4241	0-3429
	Mmax	7705	7826	8586	8857	8073	8778	7974	8809	8589	8886	8556	8795	7987	8930
	$Mmax_{10}$-$Mmax_{90}$	5525-9496	5386-9483	6776-9899	7622-9916	5028-9710	7473-9869	4530-9804	7330-9919	6986-9917	7541-9929	7100-9961	7436-9877	4348-9842	7792-9918

Changes in migration strategy

The current species distribution models simulated suitable winter quarters above the Sahara desert for many trans-Saharan migrants, changing their category from T to S (Table 4.23). The modelling techniques produced similar frequencies. However, there were some differences in which particular species were modelled as T using one modelling method and S using the other.

Table 4.23: Number of species in each category, for observed data, Climate Response Surfaces' 1960-91 simulation and Generalised Additive Models' 1960-91 simulation

	Observed	CRS	GAM
European	49	49	49
Split Strategy	107	146	147
Trans-Saharan	73	34	33
Total	229	229	229

The simulated future number of species in each category is shown in Table 4.24 while the number of species changing between categories can be found in tables 4.25-4.27 for the A1B scenario and tables A17-A19 for the A2 scenario. There was a marked difference between CRS and GAM. CRS simulated that many T migrants would become S migrants (Table 4.25-4.27). GAM, on the other hand, simulated the loss of African winter quarters for many S migrants changing their categorisation to E migrants, or simulated losses in the Western Palaearctic changing S migrants' categorisation to T (Table 4.25-4.27). Changes for each individual species can be found in the digital appendix.

Differences between present and future categories were larger for CRS than GAM (Table 4.16). These differences translate into the majority of Chi-square tests showing significant differences (Table A20) between present and all future CRS categorisation but not for GAM. There were significant differences ($p < 0.05$) between observed and expected frequencies only under GAM HadGEM 2055 and 2085 (both A1B and A2).

Table 4.24: Number of species in each category in the future. E = European migrants; S = Split strategy migrants and T = trans-Saharan migrants.

		CRS				GAM				Multi-model
	Category	Echam	GFDL	HadGEM	Mean	Echam	GFDL	HadGEM	Mean	Mean
2025 a1b	E	49	49	49	49	58	58	58	58	54
	S	162	163	163	163	141	136	145	141	152
	T	18	17	17	17	29	35	25	30	24
	Total	229	229	229	229	228	229	228	228	229
2025 a2	E	49	49	49	49	58	58	58	58	54
	S	161	162	162	162	143	139	143	142	152
	T	19	18	18	18	28	32	27	29	24
	Total	229	229	229	229	229	229	228	229	229
2055 a1b	E	49	49	49	49	57	57	56	57	52
	S	170	168	171	170	143	140	153	145	157
	T	12	14	12	13	28	32	19	26	20
	Total	229	229	229	229	228	229	228	228	229
2055 a2	E	49	49	49	49	57	57	56	57	52
	S	169	169	168	168	143	138	152	144	156
	T	13	15	14	14	29	33	20	27	21
	Total	229	229	229	229	229	228	228	228	229
2085 a1b	E	49	49	49	49	59	50	58	56	52
	S	171	169	169	170	145	148	151	148	159
	T	9	11	10	10	23	30	19	24	17
	Total	229	229	228	229	227	228	228	228	228
2085 a2	E	49	49	49	49	58	49	59	55	52
	S	172	172	173	172	146	150	153	150	160
	T	10	11	8	10	24	29	16	23	16
	Total	229	229	228	229	228	228	228	228	228

Table 4.25: Contingency table of number of species changing category for mean GAM and CRS simulations between Present day (P) and future (F) simulations for 2025 A1B scenario

	CRS			GAM		
	$F_{European}$	F_{Split}	$F_{Trans\text{-}Saharan}$	$F_{European}$	F_{Split}	$F_{Trans\text{-}Saharan}$
$P_{European}$	49	0	0	49	0	0
P_{Split}	0	145	1	9	135	2
$P_{Trans\text{-}Saharan}$	0	20	14	0	14	20

Table 4.26: Contingency table of number of species changing category for mean GAM and CRS simulations between Present day (P) and future (F) simulations for 2055 A1B scenario

	CRS			GAM		
	$F_{European}$	F_{Split}	$F_{Trans\text{-}Saharan}$	$F_{European}$	F_{Split}	$F_{Trans\text{-}Saharan}$
$P_{European}$	49	0	0	49	0	0
P_{Split}	0	146	0	8	135	4
$P_{Trans\text{-}Saharan}$	0	21	13	0	14	19

Table 4.27: Contingency table of number of species changing category for mean GAM and CRS simulations between Present day (P) and future (F) simulations for 2085 A1B scenario

	CRS			GAM		
	$F_{European}$	F_{Split}	$F_{Trans\text{-}Saharan}$	$F_{European}$	F_{Split}	$F_{Trans\text{-}Saharan}$
$P_{European}$	49	0	0	49	0	0
P_{Split}	0	145	1	1	143	3
$P_{Trans\text{-}Saharan}$	0	26	8	0	20	13

Fourteen to seventeen species were consistently simulated to change their migratory category (Table 4.28). These species did not differ (or differed very little) between emission scenarios or years. Some trans-Saharan migrants were consistently simulated to gain climatically suitable non-breeding space above the Sahara, potentially providing a mechanism for those species to decrease their migratory distance. Half the models (GAM or CRS) simulated the loss of climatically suitable non-breeding space below the Sahara for a few split strategy migrants, which may provide a mechanism for selection towards short distance migration for these species.

Table 4.28: Species with a consistent change among models in migratory strategy and their change. T = Trans-Saharan migrants, S = Split strategy migrants and E = European migrants. "Half" indicates that half the models simulates a change in strategy whilst (T) denotes those Trans-Saharan migrants that are consistently modelled as S.

	A1B		A2	
	Species	Change	Species	Change
2025	*Aquila pomarina*	T to S	*Aquila pomarina*	T to S
	Apus apus	T to S	*Apus apus*	T to S
	Caprimulgus europaeus	Half S to E	*Caprimulgus europaeus*	Half S to E
	Lanius nubicus	Half T to S	*Lanius nubicus*	Half T to S
	Lanius collurio (T)	Half S to E	*Lanius collurio* (T)	Half S to E
	Muscicapa striata	Half S to E	*Muscicapa striata*	Half S to E
	Oriolus oriolus (T)	Half S to E	*Oriolus oriolus* (T)	Half S to E
	Asio flammeus	Half S to E	*Asio flammeus*	Half S to E
	Hippolais icterina (T)	Half S to E	*Sylvia borin*	Half T to S
	Hippolais languidae	T to S	*Sylvia hortensis*	T to S
	Sylvia borin	Half T to S	*Luscinia luscinia*	T to S
	Sylvia hortensis	T to S	*Monticola saxatilis*	T to S
	Luscinia luscinia	T to S	*Tachymarptis melba*	Half T to S
	Tachymarptis melba	Half T to S	*Sterna albifrons*	Half S to E
	Sterna albifrons	Half S to E	*Otus scops*	Half S to E
	Otus scops	Half S to E		
2055	*Aquila pomarina*	T to S	*Aquila pomarina*	T to S
	Apus apus	T to S	*Apus apus*	T to S
	Caprimulgus europaeus	Half S to E	*Caprimulgus europaeus*	Half S to E
	Streptopelia turtur	T to S	*Streptopelia turtur*	Half T to S
	Lanius nubicus	Half T to S	*Lanius nubicus*	Half T to S
	Lanius collurio (T)	Half S to E	*Lanius collurio* (T)	Half S to E
	Muscicapa striata	Half S to E	*Muscicapa striata*	Half S to E
	Oriolus oriolus (T)	Half S to E	*Oriolus oriolus* (T)	Half S to E
	Sterna sandvicensis	Half T to S	*Sterna sandvicensis*	Half T to S
	Asio flammeus	Half S to E	*Asio flammeus*	Half S to E
	Hippolais icterina (T)	Half S to E	*Hippolais icterina* (T)	Half S to E
	Sylvia hortensis	T to S	*Sylvia hortensis*	T to S
	Luscinia luscinia	T to S	*Luscinia luscinia*	T to S
	Monticola saxatilis	T to S	*Monticola saxatilis*	T to S
	Tachymarptis melba	Half T to S	*Tachymarptis melba*	T to S
	Sterna albifrons	Half S to E	*Sterna albifrons*	Half S to E
	Otus scops	Half S to E	*Otus scops*	Half S to E
2085	*Aquila pomarina*	T to S	*Aquila pomarina*	T to S
	Apus apus	T to S	*Apus apus*	T to S
	Streptopelia turtur	T to S	*Streptopelia turtur*	T to S
	Emberiza hortulana	Half T to S	*Emberiza hortulana*	T to S
	Lanius nubicus	Half T to S	*Lanius nubicus*	Half T to S
	Ficedula hypoleuca	T to S	*Ficedula hypoleuca*	T to S
	Ficedula semitorquata	Half T to S	*Ficedula semitorquata*	T to S
	Asio flammeus	Half S to E	*Asio flammeus*	Half S to E
	Acrocephalus scirpaceus	Half T to S	*Acrocephalus scirpaceus*	Half T to S
	Sylvia hortensis	T to S	*Sylvia hortensis*	T to S
	Sylvia nisoria	Half T to S	*Sylvia nisoria*	Half T to S
	Luscinia luscinia	T to S	*Luscinia luscinia*	T to S
	Monticola saxatilis	T to S	*Monticola saxatilis*	T to S
	Tachymarptis melba	T to S	*Tachymarptis melba*	T to S

Residency

Changes in species' proportion of resident cells can be found in Tables A21-23. These show differences in the proportion of each species' range that resident cells form. The proportions did not vary much between different future simulations. The average variation was 2% for both CRS and GAM as well as between the two modelling techniques. The anomalies did not vary much between simulations either. The multi-model mean anomalies of resident cells for the mean of species are shown in Table 4.29. This shows that the change in proportion of resident cells was greater for European migrants. For split strategy migrants and trans-Saharan migrants, very little range became suitable for both wintering and breeding. Figure 4.25 shows the range of anomaly values for each migratory category and shows that European migrants vary much more than the other groups.

Table 4.29: Mean proportion change in resident cells for all species and for each migratory group

		A1B			A2	
All species	2025	2055	2085	2025	2055	2085
increase	0.17	0.16	0.15	0.18	0.17	0.16
decrease	0.13	0.13	0.13	0.13	0.13	0.13
European						
increase	0.27	0.26	0.24	0.27	0.27	0.26
decrease	0.29	0.31	0.32	0.32	0.31	0.32
Split strategy						
increase	0.09	0.09	0.09	0.09	0.09	0.09
decrease	0.09	0.10	0.09	0.09	0.10	0.09
Trans-Saharan						
increase	0.01	0.01	0.01	0.01	0.01	0.01
decrease	0.06	0.06	0.06	0.06	0.06	0.06

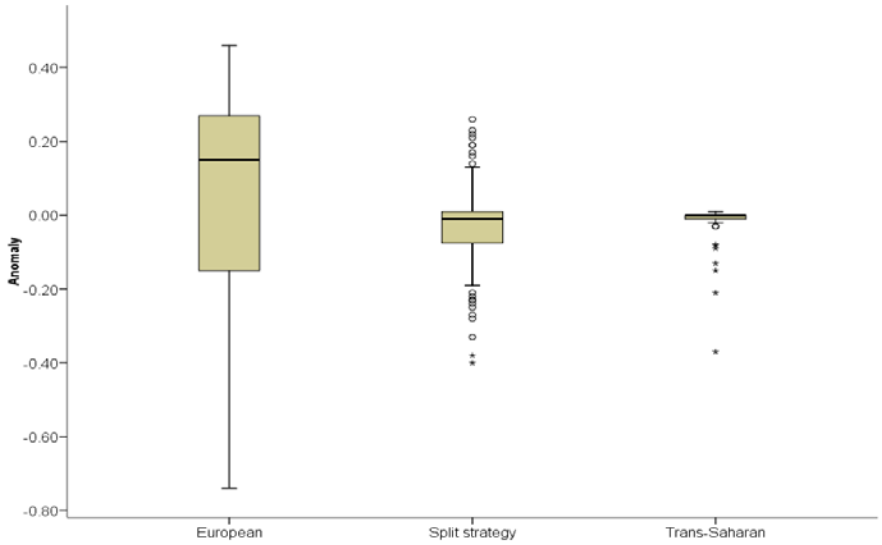


Figure 4.25: Anomalies between present and future proportion resident cells for 2055 A1B. The anomalies for the other time periods are virtually the same and, therefore, are not shown here.

The proportion of migrants in each group either becoming more resident (positive anomalies), less resident (negative anomalies) or no change are shown in Table 4.30.

Table 4.30: Proportion of species in each migratory group (European, Split strategy and Trans-Saharan migrants) that have positive anomalies (more resident), negative anomalies (less resident) and show no change in the proportion of resident cells.

		2025			2055			2085		
		Europe	Split	Trans	Europe	Split	Trans	Europe	Split	Trans
A1B	% more resident	57	20	1	61	20	1	61	20	1
	% less resident	43	39	10	39	38	10	39	38	10
	% no change	0	41	89	0	42	89	0	42	89
A2	% more resident	57	20	1	61	21	1	55	20	1
	% less resident	39	39	10	39	36	10	39	37	10
	% no change	4	41	89	0	44	89	6	43	89

The results from Table 4.30 show that European short-distance migrants have a large proportion of species potentially becoming more sedentary, with 55-61% of European migrants increasing the proportion of resident cells in their range. The majority of trans-Saharan migrants (89%) showed no change in the proportion of resident cells. The changes for the remaining 11% arise from changes to those species that also have populations that breed south of the Sahara. Split strategy migrants showed a fairly equal distribution of change in proportion of resident cells though fewer were simulated to become more resident in the future.

The models simulated that eight species (*Circus pygargus*, *Hieraaetus pennatus*, *Apus Apus*, *Merops apiaster*, *Motacilla flava*, *Acrocephalus arundinaceus*, *Sylvia hortensis*, *Cercotrichas galactotes*) would gain 'resident cells' where before they had (virtually) none. These new areas suitable for both breeding and over-wintering are found either in Portugal, Cape Verde islands, or North Africa (Figure 4.26 and digital appendix).

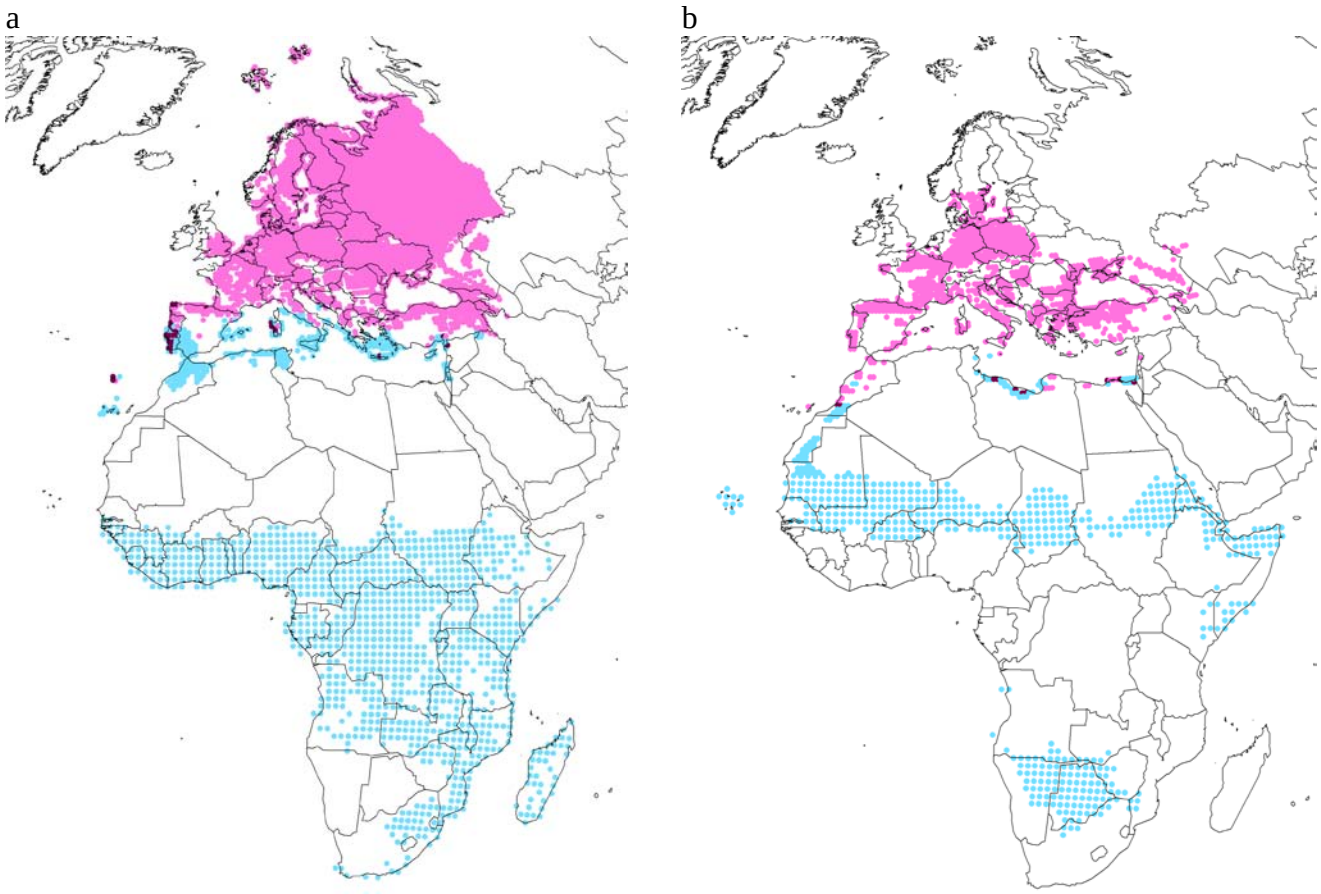


Figure 4.26: Simulated future resident areas by Climate Response Surface simulations using Echam 2085 A1B scenario of a) *Acrocephalus arundinaceus* and b) *Sylvia hortensis*; Pink = breeding range, blue = non-breeding range and purple = resident range

Figure 4.27 shows the range of proportional change in resident cells separated by breeding biome. In all time periods, change in proportion of residency differed between biomes (A1B: $H_6 = 23.09$, $p < 0.005$ for 2025; $H_6 = 23.87$, $p < 0.005$ for 2055; $H_6 = 23.70$, $p < 0.005$ for 2085. A2: $H_6 = 24.25$, $p < 0.001$ for 2025; $H_6 = 25.18$, $p < 0.001$ for 2055; $H_6 = 23.77$, $p < 0.005$ for 2085). Despite some variation, species residing in Temperate Broadleaf and Mixed Forest showed no change in the proportion of resident cells. Species residing in dry environments increased their resident cells on average (Fig. 4.27: Biome 12 and 13) whilst other species decreased on average their number of resident cells. Tundra-residing species decreased their proportion of resident cells.

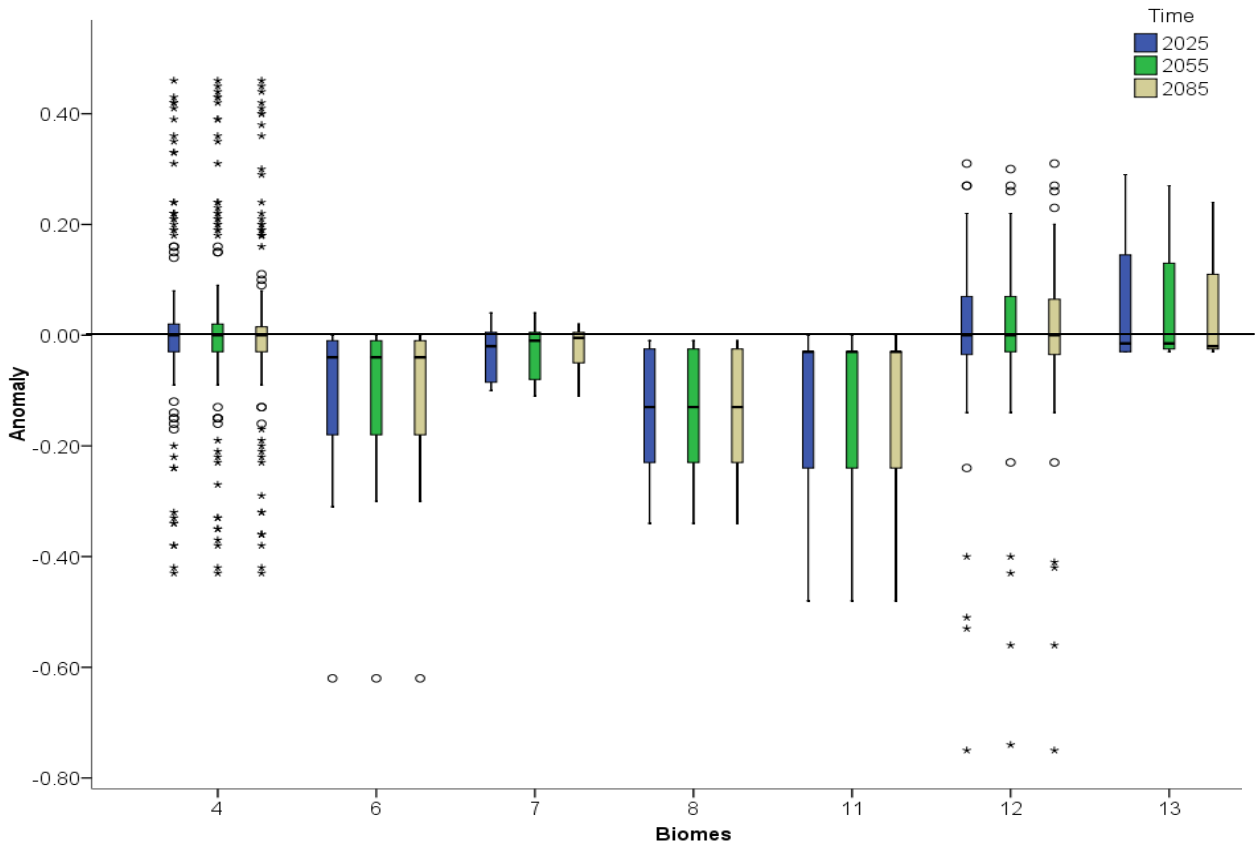


Figure 4.27: Anomalies between present and future proportion resident cells for A1B scenario separated by biome for the different time-slices. Biomes: 4 = Temperate Broadleaf and Mixed Forest; 6 = Boreal Forest/Taiga; 7 = Tropical and Subtropical Grassland, Savannah and Scrubland; 8 = Temperate Grassland, Savannah and Scrubland; 11 = Tundra; 12 = Mediterranean Forest, Woodland and Scrubland; 13 = Desert and Xeric Scrubland

4.3.4 Discussion

The results suggest that long-distance migrants will fare worse than short-distance migrants under predicted climate change. The relative range extent of split strategy migrants, those species that have populations that overwinter both South of the Sahara and in the Western Palaearctic, showed reduced range on the breeding grounds, while trans-Saharan migrants showed the lowest increase on the non-breeding grounds (as a mean, all groups increase their non-breeding range extents). These two groups also had the lowest overlap between simulated current and future range extents. Trans-Saharan migrants also had a greater shift in range on the non-breeding grounds. Interestingly, trans-Saharan migrants are projected to lose a greater proportion of their current range on their non-breeding grounds, whilst split strategy migrants would lose a greater proportion on their breeding grounds. These results suggest that, if the future climate projections are part of an on-going trend, the mechanism of current decline of trans-Saharan migrants is the climatic conditions on the non-breeding grounds. This hypothesis will be explored in Chapter 5 as population trends are correlated with current and future climatic change.

Changes in mean migration distances showed no systematic variation among migrant groups. However, trans-Saharan migrants did have significantly reduced minimum migration distances and increased maximum migration distances. Increased maximum distances could have severe consequences for migrants as extra energy would be required to fuel the birds (Doswald *et al.*, 2009) and more time spent migrating might also decrease fitness. Reduced minimum migration distances, however, would increase a species' fitness. Reduced migration distance is simulated by new suitable non-breeding climate space closer to the breeding grounds. These newly suitable areas may be very important for long-distance migrant birds. Indeed, Cotton (2003) suggested that long-distance migrant birds would have to shift their non-breeding grounds closer to the breeding grounds to receive the right cues on when to migrate under a changing climate. Closer non-breeding quarters may also change species' migratory behaviour. However, even if not utilised as non-breeding areas, these new suitable areas in between the breeding and non-breeding range may be useful as stopover areas.

Changes in simulated future species richness of each migratory group showed similarities between groups, though each group exhibited different trajectories through time. Changes in species richness of each group, although interesting, does not tell us much about effects on turnover or community reassembly. Changes in the proportion of species in each group in each grid cell are far more revealing. Overall, trans-Saharan migrants were projected to increase in

proportional richness, compared to other groups on the breeding grounds, whilst split strategy migrants were projected to increase to the detriment of other groups on the non-breeding grounds. There were also marked spatial differences. On the breeding grounds, patterns of change in proportion of migrant groups were similar to results found by Lemoine *et al.* (2007), though they only had two groups of migrants: the proportion of long-distance migrants increased in most of Europe, most strongly in Southern Europe, whilst the proportion of short-distance migrants decreased in Europe, especially in Scandinavia and Spain. My results showed more specifically (digital appendix) that the proportion of trans-Saharan migrants increased in the North of Europe, whilst split strategy migrants increased in the South (and on their African breeding grounds); European migrants increased in between. On the non-breeding grounds, the proportion of European migrants decreased except in Scandinavia and was replaced by split strategy migrants and a few trans-Saharan migrants. Trans-Saharan migrants decreased on the African winter quarters in proportion to split strategy migrants but increased in proportion in the Mediterranean region. These results suggest two mechanisms of change occurring: species' turnover or community reassembly as species' ranges are shifted, and change in migration strategy (adaptation).

Change in migration strategy

My results indicated potential changes in migration strategy for some species. Although the different modelling methods showed similarities for some species, they also showed marked differences. Under both modelling techniques, though more so for CRS, trans-Saharan migrants gained non-breeding climatic space above the Sahara, changing their categorisation to split strategy migrants. These simulated changes may not necessarily mean changes in migratory behaviour. GAM, on the other hand, predicted that some S migrant species would lose their winter quarters across the Sahara and become E migrants, and some S migrants might become solely T migrants. Loss of suitable climatic space in an area may be a mechanism for changing migratory strategy especially for a partial migrant. However, it may lead to population declines if species cannot adapt or evolve.

Changes in the number of resident cells in proportion to the rest of their range showed that about 60% of short-distance migrants were likely to become more resident. Split strategy migrants did not change or decreased the amount of resident range in equal number, while a

minority of about 20% increased their proportion of resident range. Trans-Saharan migrants' range proportions did not change for the majority (89%). These results suggest that short-distance migrants and some split strategy migrants may become more resident under future climate change as conditions become suitable on the breeding grounds all year round. Many *Phylloscopus collybita*, *Phoenicurus ochruros* and *Turdus merula* are already showing evidence of changes in migratory behaviour arising from milder winters (Birkhead, 2008). My results also suggest that species residing in dry environments (Mediterranean region) are more likely to become more resident than other species.

Schaefer *et al.* (2008) modelled changes in migratory propensity (proportion of potentially migratory species in a grid cell) and migratory activity (proportion of potentially migratory species that actually migrate) to find out the future proportion of migratory species and the mechanisms behind these changes. They used changes in migratory propensity as a measure of community reassembly and changes in migratory activity as a measure of adaptation in species. Their future simulations produced increases in proportion of migratory species in southern Europe, which were due to community reassembly, and decreases in proportion of migratory species in the northern Europe attributed to adaptation. My results support these findings. However, Schaefer *et al.* (2008) concluded that community reassembly would lead to a more even spread of migrants across Europe and therefore climate change posed no general threat to migratory species. This view does not take into account multiple factors such as species' winter range, ability to adapt or even shift ranges. Moreover, Henningsson and Alestram (2008) showed that bird community heterogeneity and species' spatial turnover on the breeding grounds was dependant on non-breeding habitat and migratory distance, which might limit how range changes occur with climate change.

4.3.5 Conclusion

This study compared the impacts of climate change between migrant species' groups and investigated potential changes in migratory strategy. The results from the future simulations suggest that:

1) Trans-Saharan migrants may fare worse under climate change. The results showed low overlap, lower range extent, large range shifts for trans-Saharan migrants but only on their non-breeding grounds, whilst split strategy migrants were simulated to have low overlap and low range extent on the breeding grounds.
2) Short-distance migrants may be better off than long-distance migrants as the measures of change were better for these species. However, species richness changes and community reassembly did not appear to favour the European short-distance migrants.
3) Short-distance and split strategy migrants may become more resident. The results show an increase in the proportion of resident cells for short-distance and some split strategy migrants. Short-distance strategies were simulated to become more widespread through new winter ranges in the Western Palaearctic and loss of climatic suitability in areas below the Sahara desert.

5. Species' vulnerability to climatic change

The forecast future range change for many species in response to climate change may have important consequences for the survival of many populations. Population abundance and range size are not independent (Lawton, 1993) and some studies have documented a link between population declines and range contractions (Fuller *et al.*, 1995; Lister and Stuart, 2008; Treinys *et al.*, 2008), although the rate of decline may be different from the rate of range contraction (Shoo *et al.*, 2005; Akçakaya *et al.*, 2006; Rhodes *et al.*, 2008).

Species have already responded to the current climatic change by changes in phenology and range expansion (Parmesan and Yohe, 2003), as well as range contraction (Thomas *et al.*, 2006). It is more difficult, however, to attribute changes in population to climatic change because other factors also impact on species' populations (see Newton, 1998). A few studies have attempted to find a link between population change and climate. These studies demonstrate the association between population change and climate, rather than a demonstration of cause and effect. For instance, Juillard *et al.* (2004) found that birds with south-biased distributions were doing better than those with north-biased distributions in France. Treinys *et al.* (2008) also found a north-south gradient in changes in *Cicona nigra* populations in central Europe. Species may differ in their sensitivity to climate change due to their ecological characteristics, such as their migratory strategy (see section 4.3) or habitat preferences (Juillard *et al.*, 2003). It is important to determine which species are most likely at risk.

In the first part of this chapter, an index of climate change impact on migratory species is developed. This index is a measure of species' sensitivity to climate change. I investigate which species are most likely to suffer from climatic change and which are the least likely to do so in relation to their ecological characteristics. This index is based on the projected effects of climate change on the distribution of migratory birds.

Inferences made using changes in species' ranges, as projected by species distribution models (SDM), are often used as a proxy for changes in species' populations and extinction risk (Bomhard *et al.*, 2005; Thuiller *et al.*, 2005). However, this assumption is rarely tested. Finding out whether SDM can be used as a proxy for changes in population is necessary in order to: a) validate in part the use of these models (in part only as the primary purpose is to depict changes in range not population) and b) to provide a measure of the extent to which these models can be used to make inferences on the extinction risk of species.

Green *et al.* (2008) demonstrated that SDM can be used to retrodict past population changes. Furthermore, Gregory *et al*. (2009) showed that recent population changes reflected the projected effects of climatic change. Their analysis provides the basis of an indicator of the impact of climate change on birds. However, as seen in the previous chapter, climate change may impact on migratory species differently.

Species' abundances change for a variety of reasons. Habitat loss or degradation and species' persecution are known to cause decreases in population size. Severe weather is also a factor in species' mortality. Indeed many migratory bird populations suffered during the Sahelian drought during the 1970s (Peach *et al.*, 1991). It is reasonable therefore to expect that climate change may affect population size to a certain degree.

In the second part of this chapter, factors determining recent population trends of Afro-Palaearctic migratory birds are examined. Population changes may be associated with species-specific characteristics such as habitat, biome, migratory strategy or taxonomy. Indeed, both Gregory *et al.* (2007) and Seosane and Carrascal (2008) showed that bird population trends could be explained by species' ecological traits. Furthermore, Bauer *et al.* (2008) found that passerines and non-passerines differed in their changes in abundance. Changes in climatic suitability on both breeding and non-breeding grounds are then related to population trends to discover whether climate is a factor in population changes and whether climatic models can be used to make inferences about future extinction risk.

In the final part of this chapter, future climate change risk is related to recent population change. I examine whether current population trends go in the direction predicted by the index. Furthermore, the population trends of species most at risk of climate change are examined, allowing for a discussion on the likelihood of populations' vulnerability to climatic change.

5.1 Index of impact of future climatic change on species

1.5.1 Introduction

Climate change is projected to affect species in many different ways, including their population size, phenology, demography and distribution (see Chapter 2). In the previous chapter, measures of distributional change caused by climatic change were calculated for migratory birds. These measures demonstrated the potential impacts of climate change on migratory birds in general. Knowing the magnitude and direction of change for the vast majority of species is interesting but does not allow for focused conservation efforts, especially because there is a great variation in species' responses to climate change (section 4.2). Conservationists need to know which species are the most vulnerable to climate change. The IPCC (2001) defines vulnerability to climatic change as "the extent to which a natural or social system is susceptible to sustaining damage from climate change" (p.21) and states that "vulnerability is a function of the character, magnitude and rate of climate change and the variation to which a system is exposed, its sensitivity, and its adaptive capacity" (p.21).

The IUCN Red list uses range size as one of their criteria to assess a species' vulnerability/extinction risk (IUCN, 2001; IUCN, 2006). Consequently, the measures of change in species' distributions as a result of climate change provide us with a measure of species' sensitivity to climatic change. To assess a species' vulnerability, the likelihood of the projected changes impacting on the species has to be taken into account. Assessing this is very difficult because information on the adaptive capabilities of many species do not exist. Furthermore, much of the projected change has never been experienced before (Overpeck *et al.*, 1992; Jackson and Overpeck, 2000; Hobbs *et al.*, 2006; Williams and Jackson, 2007). Current evidence suggests that many birds and migrant birds are responding to climatic change (see Chapter 2). For example, species are expanding their ranges polewards (Parmesan and Yohe, 2003) as models of distribution change project (Chapter 2 and section 4.2) and the declines of several bird populations have been linked to climatic change (Baillie and Peach, 1992; Julliard *et al.*, 2004; Beale *et al.*, 2006; Sanderson *et al.*, 2006). The projected changes resulting from climate change are therefore very likely to affect species, especially when other considerations interacting with climate change such as habitat or land-use change are taken into account (Erasmus *et al.*, 2002; Bomhard *et al.*, 2005; Okes *et al.*, 2008).

Sensitivity or vulnerability indices for the impact of climate change on species are rare in the literature and no accepted methodological framework exists. Three studies were found

that attempted to quantify sensitivity or vulnerability of species to climatic change. Matsui *et al.* (2004) calculated a sensitivity index based on the difference in simulated probability of occurrences of *Fagus crenata* between current and future simulations and then used the reciprocal of the predicted probabilities as a vulnerability index. This provides a spatial element to a species' vulnerability to climate change, whereas merely quantifying changes in range size for example does not. However, probability of occurrence obtained from a model is linked to species' prevalence (Lui *et al.*, 2005; Jimènez-Valverde and Lobo, 2007) which was not taken into account in the study, potentially biasing the results.

Berry *et al.* (2006) used measures of range change to calculate four 'sensitivity indicators'. They used a six-point scoring system to create the sensitivity indicators. These indicators were then combined to create two vulnerability indices based on whether or not the range expansion projected under climatic change was included. Although their conceptual index is attractive, it potentially suffers from their use of four highly correlated indicators. All the indicators related to an aspect of change in range size (new climate space, lost climate space, overlap and overall range size) which were then added together.

Laidre *et al.* (2008) quantified the sensitivity of Arctic marine mammals to climate-induced habitat change, using an expert-based scoring system on variables such as diet, migration or site-fidelity, that were likely to influence the response and vulnerability of Arctic marine mammals to climate change. Their sensitivity index assumes that all variables have equal influence on species. Their study is the first attempt objectively to quantify species' sensitivity to climate change that includes many aspects of species' ecology.

Given the paucity of studies that address species' vulnerability and the variety in their methodology, I created a vulnerability index for migrant birds using the measures of change calculated in the previous sections. Changes in range size, overlap between simulated current and future range, and changes in migration distance are likely to affect migrant birds. Reduction in the size of climatically suitable areas can affect populations negatively; responses will be seen either through changes in distribution or population numbers. A projected increase in range size may allow for population increase as well as range expansion. However, species have to be able to make use of new range. Physical, genetic, ecological or historical barriers may prevent a species from occupying newly suitable range. Moreover, even if a species is capable of expanding its range, vegetation and species may be slow to respond (Chapin III and Starfield, 1997; Menendez *et al.*, 2006). Therefore, overlap is an important measure of change as it quantifies the amount of current range that is still suitable in the future and provides a "worst case scenario" of remaining range. The creation of a vulnerability index for migrants is potentially complex as environmental conditions, and how

climate change will affect these, may be different on the seasonal ranges. However, conditions on either one of their ranges are likely to have impacts on species (Gordo and Sanz, 2008) and as argued in section 4.2.3, cannot be independent of each other. Therefore the least favourable measure of change between breeding and non-breeding, i.e. the lowest value of overlap or relative range extent between the two goal areas, was used for the index. Furthermore, migration itself is a risk-filled endeavour because species need to have adequate fuel and/or stopover sites (Newton, 2006). Increases in migration distance are thus likely to put additional stress on species. The vulnerability index also takes change in migration distance into account. Having created a vulnerability index for migrant bird species, the questions then are:

1) Which species are most vulnerable?
2) Are there groups that are more vulnerable than others?
3) What elements affect a species' vulnerability to climate change?
4) Which factors (overlap, range extent or migratory distance) contribute most to species' vulnerability?

These questions are investigated in this section by testing the influence of factors on vulnerability scores, such as a species' habitat preference or migration strategy and investigating whether certain measures of change contribute more to a species' vulnerability score. Furthermore, I discuss the contribution of climate change impacts on already threatened species, i.e. those on the IUCN Red List. The vulnerability index is not, however, used in any way to classify or reclassify species in terms of their extinction risk as defined by IUCN red list criteria (see Akçakaya *et al.*, 2006).

5.1.2 Methods

Vulnerability index

The multi-model mean measures of projected change due to climate change from section 4.2 were used to find, for each species, the minimum relative range extent (R), minimum overlap (O) and proportional change in migratory distance (PM) between present and future climate change for 2025, 2055 and 2085 A1B and A2 (see section 4.2). Minimum values refer to the minimum between the breeding and non-breeding measures. Species were then ranked separately for these three measures so that the species with the lowest R had the highest ranking, the lowest O had the highest ranking and the species with the highest PM had the highest rank. These three ranked values were then converted to scores using an ordinal scale of 1-10 for species in the 10 deciles such that species with an R, or O or PM score of 10 were the most vulnerable. For each species, a Vulnerability score (Vscore) was calculated by adding R, O and PM scores. The minimum Vscore was therefore 3 and the maximum Vscore 30. Species with Vscores of 26-30 can be thought of as extremely vulnerable, Vscores 21-25 as highly vulnerable, 16-20 as vulnerable, 11-15 as moderately vulnerable, and 3-10 as least vulnerable (see Table 5.1).

Analyses

Vscores were normalised by logit transformation because a Kolmogorov-Smirnov test indicated that Vscores were not normal ($p < 0.001$). Differences in vulnerability scores between 2025, 2055 and 2085 time-slices were tested by repeated-measures ANOVA[1] to see if species as a whole significantly changed their Vscores through time.

The effects of a species' habitat, biome, tolerance and migratory strategy (defined in Table 3.15 and Fig 3.5) and interaction between habitat and biome or tolerance and biome were tested using ANOVA for each time-slice and scenario with Tukey's *post hoc* tests.

The most important factor contributing to a species' Vscore, was found by analysing which of the three categories or 'indicators' (R, O or PM) carried the most weight in the score. If either of these categories contributed to the score by a difference of 3 or greater than both of the other two factors, it was deemed to be contributing 'most' to the Vscore. Chi-square tests were conducted to examine if the frequency of the most contributing indicator was evenly spread out, while Friedman tests examined whether categories changed between each time-slice. Chi-square tests were then conducted to determine if the contributing

[1] Mauchley's tests are in Appendix II as stated on p.75.

indicators were affected by species' ecology (habitat, biome, breadth of niche (tolerance), or migratory category).

IUCN Red list and Vscores

Species found on the IUCN red list were examined in terms of their vulnerability to climate change. Of the nineteen migratory birds found on the red list in categories above 'least concern', two species are categorised as "endangered", five as "vulnerable" and the rest as "near threatened". Endangered (EN) species are those facing a very high risk of extinction in the wild, vulnerable (VU) a high risk of extinction and the near threatened (NT) category is assigned to species that do not qualify for critically endangered (CR), EN or VU but are close to qualifying or are likely to qualify for a threatened category in the near future (IUCN, 2001; IUCN, 2006).

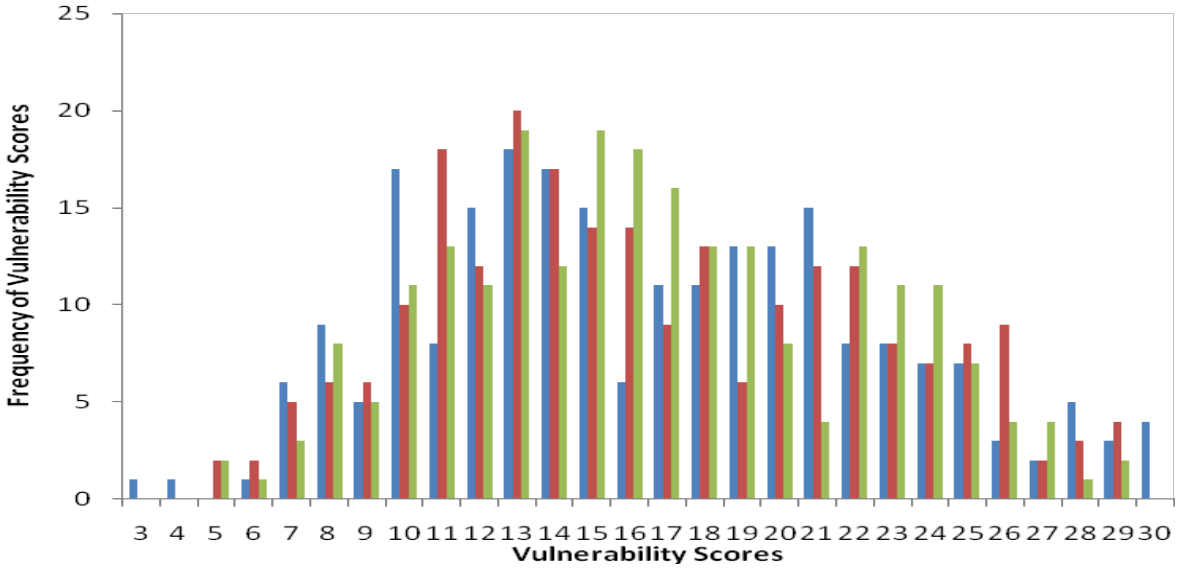
5.1.3 Results

The distribution of Vscores showed a larger number of species with mid-range values (Fig. 5.1). The concentration of high Vscores was slightly less by the end of the century compared with beginning and mid 21st century. The number of species in each category of Vscore shows that the majority of migrant birds are potentially only moderately vulnerable to the effects of climate change (Table 5.1). Eleven to eighteen species were classified as extremely vulnerable according to their Vscores.

Table 5.1: Number of species in each Vulnerability score category; VU = Vulnerable.

Score	**Definition**	**2025**		**2055**		**2085**	
		A1B	A2	A1B	A2	A1B	A2
V3-V10	least VU	40	38	31	32	30	31
V11-V15	moderately VU	73	70	81	78	74	72
V16-V20	VU	54	56	52	52	68	69
V21-V25	high VU	45	47	47	50	46	46
V26-V30	extremely VU	17	18	18	17	11	11

a)



b)

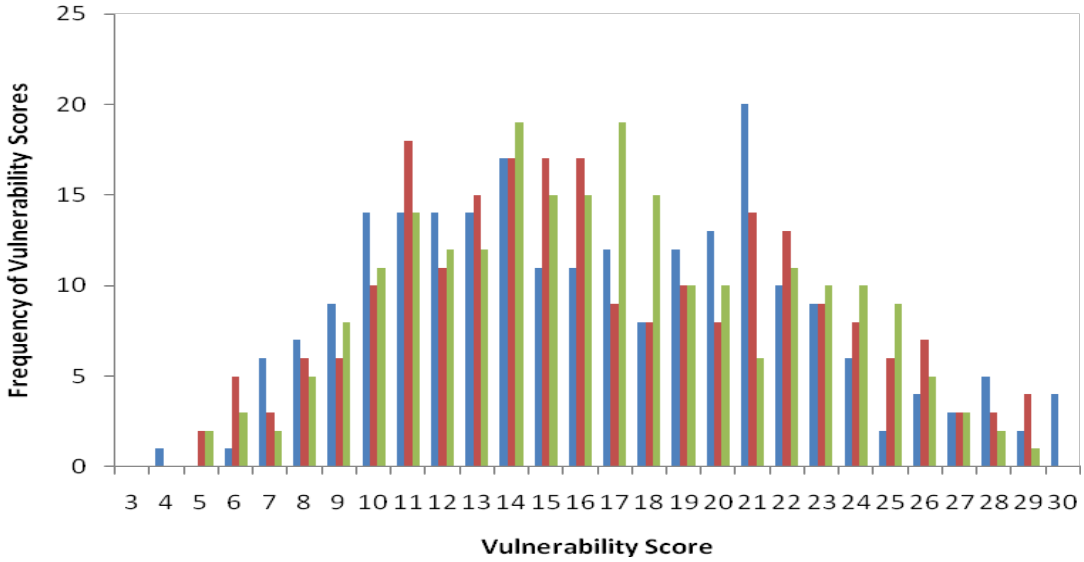


Figure 5.1: Frequency distribution of Vulnerability Scores for a) the A1B scenario and b) the A2 scenario. Blue represents 2025, red 2055 and green 2085.

The indicators which contributed most to species' low- to mid-range Vscores were not evenly spread out among species (Table 5.2). PM was more often important in contributing to Vscores than were the other indicators. R and O between current and future simulations become more important (in contributing towards a higher Vscore) towards the end of the century. However, there were no significant differences in category distribution between periods (A1B: $\chi_2 = 1.16$, $p = 0.560$; A2: $\chi_2 = 0.56$, $p = 0.754$).

Table 5.2: Number of times an indicator was more important than others in the Vulnerability scores and results of Chi-square test. *denotes level of significance.

Indicator	**2025**		**2055**		**2085**	
	A1B	A2	A1B	A2	A1B	A2
Proportion migratory distance	44	47	43	45	38	40
Percentage overlap (current-future)	11	13	8	10	12	17
Relative range extent	10	10	11	13	20	17
χ^2	34.55^{***}	36.20^{***}	36.41^{***}	33.20^{***}	15.20^{**}	14.29^{**}

Certain factors concerning species' ecology did affect which indicators contributed most to a species' Vscore. The breadth of a species' niche (tolerance) did not make species more vulnerable to a specific indicator. Under the A1B emissions scenario, species' habitat (2025: $\chi^2_{18} = 29.14$, $p = 0.047$; 2055: $\chi^2_{18} = 35.95$, $p = 0.007$; 2085: $\chi^2_{18} = 38.20$, $p = 0.004$) contributed to vulnerability for certain indicators. Forest species were more likely to be vulnerable due to smaller future range extents, coastal and wetland species were more likely to be affected primarily by small overlap, whilst forest and wetland species were more likely to be affected by increases in average migratory distance.

Biome also affected which indicators contributed most to Vscores except for breeding biome in 2025 (2025: breeding: $\chi^2_{21} = 18.67$, $p = 0.606$, non-breeding: $\chi^2_{15} = 38.22$, $p = 0.001$; 2055: breeding: $\chi^2_{21} = 32.93$, $p = 0.047$, non-breeding: $\chi^2_{15} = 36.94$, $p = 0.001$; 2085: breeding: $\chi^2_{21} = 39.51$, $p = 0.009$, non-breeding: $\chi^2_{15} = 36.38$, $p = 0.002$). On the breeding grounds, species inhabiting temperate broad leaf and mixed forest or taiga were more vulnerable to changes in range extent. Species inhabiting temperate coniferous forest or the Mediterranean biome were more likely to suffer from low overlap between simulated current and future range and greater migration distances. On the non-breeding grounds, species inhabiting temperate broadleaf and mixed forests or tropical/subtropical grasslands, savannah or scrubland were more affected by changes in relative range extent than species residing in other biomes. Species in the drier biomes (Mediterranean forest, woodland and scrub or desert and xeric scrubland) were more likely to have high Vscores based on overlap between simulated current and future range. Proportional change in migratory distance was a contributing indicator mainly to species residing in tropical/subtropical grasslands, savannah or scrub.

Species' migratory category influenced which factor contributed most to a species' Vscore for the 2025 and 2055 time-slice but not 2085 (2025: $\chi^2_6 = 18.10$, $p = 0.006$; 2055: $\chi^2_6 = 13.59$, $p = 0.035$; 2085: $\chi^2_6 = 6.43$, $p = 0.375$). European and split strategy species were more likely to have a predominant contributing indicator whilst Trans-Saharan species were more likely to have Vscores built with an even spread of indicators.

Under the A2 scenario, species' habitat characteristics affected which indicators contributed most to a species' Vscore. Non-breeding biome, however, affected which indicator contributed most to the Vscores (2025: $\chi^2_{15} = 25.93$, $p = 0.039$; 2055: $\chi^2_{15} = 46.79$, $p = 0.000$; 2085: $\chi^2_{15} = 35.76$, $p = 0.002$) as under the A1B scenario. Breeding biome was only important for the 2085 time-slice ($\chi^2_{21} = 37.21$, $p = 0.016$) with similar results to the A1B scenario. Similarly to A1B scenario, migratory category was important for 2025, 2055 but not 2085 (2025: $\chi^2_6 = 13.27$, $p = 0.039$; 2055: $\chi^2_6 = 17.59$, $p = 0.007$; 2085: $\chi^2_6 = 5.03$, $p = 0.542$).

Table 5.3-5.5 lists the species found in each Vulnerability category (along with contributing indicator) under the A1B scenario whilst the A2 scenario can be found in Tables A24-26. There is a mix of species (passerines and non-passerines) in each category, although more non-passerines occur in the extremely vulnerable category. Species in each category are similar across emission scenarios. Those in the extremely vulnerable category are very similar between 2025 and 2055 but are slightly different for 2085: Six species out of eleven for the A1B scenario and two out of eleven for the A2 scenario are common to both 2085 and 2055.

Table 5.3: Species in each vulnerability (VU) category according to their vulnerability scores (V) for 2025 A1B scenario**.** Most contributing indicator (R: relative range extent, O: overlap, PM: proportional change in migratory distance) , indicator with a difference of either 3 or more from other indicators, listed next to relevant species.

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
Acrocephalus arundinaceus	*Acrocephalus paludicola*	*Accipiter nisus* (PM)	*Anas crecca*	*Acrocephalus scirpaceus*
Alauda arvensis	*Actitis hypoleucos* (R)	*Acrocephalus palustris*	*Botaurus stellaris*	*Anas penelope*
Anas querquedula	*Anthus campestris*	*Acrocephalus schoenobaenus* (R)	*Calidris minuta*	*Apus affinis*
Anthropoides virgo (O)	*Anthus trivialis*	*Anas acuta*	*Calidris temminckii*	*Bubulcus ibis*
Ardea cinerea	*Apus pallidus* (PM)	*Anas clypeata* (PM)	*Caprimulgus europaeus*	*Charadrius morinellus*
Asio flammeus (R)	*Aquila clanga*	*Anas platyrhynchos* (PM)	*Caprimulgus ruficollis*	*Chlidonais hybridus*
Asio otus (PM)	*Ardea purpurea* (PM)	*Anthus cervinus*	*Carpospiza brachydactyla*	*Ciconia nigra*
Calandrella brachydactyla	*Ardeola ralloides* (PM)	*Anthus pratensis*	*Charadrius hiaticula*	*Egretta alba*
Cercotrichas galactotes	*Aythya nyroca* (PM)	*Anthus spinoletta*	*Ciconia ciconia*	*Falco columbarius*
Charadrius alexandrinus (O)	*Burhinus oedicnemus* (PM)	*Apus apus* (R)	*Emberiza cia*	*Milvus migrans*
Childonias niger	*Buteo buteo* (O)	*Aquila heliaca*	*Emberiza caesia*	*Neophron percnopterus*
Circus pygargus	*Buteo rufinus* (PM)	*Aquila nipalensis*	*Emberiza cineracea*	*Oenanthe xanthoprymna*
Clamator glandarius	*Carduelis cannabina* (PM)	*Aquila pomarina*	*Falco cherrug*	*Pelecanus onocrotatus*
Coccothraustes coccothraustes	*Carduelis carduelis* (PM)	*Arenaria interpres*	*Ficedula semitorquata*	*Porzana parva*
Coturnix coturnix	*Carduelis chloris* (PM)	*Aythya ferina (PM)*	*Gallinago gallinago*	*Sterna sandvicensis*
Delichon urbica	*Cettia cetti* (PM)	*Aythya fuligula*	*Geronticus ermita*	*Tachybaptus ruficollis*
Emberiza schoeniclus	*Chlidonias leucopterus*	*Calidris alpina*	*Hippolais icterina*	*Turdus torquatus*
Erithacus rubecula (R)	*Cicaetus gallicus*	*Charadrius dubius*	*Irania gutturalis*	
Falco naumanni	*Circus cyaneus*	*Circus aeruginosus*	*Lanius nubicus*	
Falco peregrinus	*Columba palumbus*	*Circus macrourus*	*Larus fuscus*	
Fringilla coelebs	*Coracias garrulus*	*Egretta garzetta*	*Larus ribundus*	
Glareola praticola (O)	*Crex crex (PM)*	*Emberiza hortulana*	*Limosa lapponica*	
Himantopus himantopus	*Cuculus canorus*	*Falco eleonorae*	*Locustella naevia*	
Hippolais languidae (PM)	*Falco subbuteo*	*Falco vespertinus*	*Lymnocryptes minimus*	
Hippolais pallida (PM)	*Falco tinnunculus*	*Ficedula albicollis*	*Melanocorypha bimaculata*	
Hirundo rustica	*Ficedula hypoleuca*	*Gelochelidon nilotica*	*Merops apiaster*	
Lanius senator (PM)	*Gallinago media*	*Grus grus*	*Monticola saxatilis*	
Luscina megarhynchos (PM)	*Gallinula chloropus*	*Hieraaetus pennatus*	*Motacilla cinerea* (PM)	
Marmaronetta angustirostris (O)	*Gyps fulvus*	*Hirundo daurica*	*Muscicapa striata*	

Table 5.3 continued

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
Monticola solitarius	*Hippolais polyglotta* (PM)	*Jynx torquilla*	*Numenicus phaeopus*	
Nycticorax nycticorax (PM)	*Hirundo rupestris*	*Lanius collurio*	*Oriolus oriolus*	
Oenanthe hispanica	*Ixobrychus minutus* (PM)	*Lanius minor*	*Otus scops*	
Oenanthe isabellina	*Larus genei* (O)	*Limosa limosa*	*Passer hispaniolensis*	
Regulus regulus (R)	*Limicola falcinellus* (O)	*Melanocorypha calandra* (PM)	*Pluvialis apricaria*	
Streptopelia turtur	*Locustella fluviatilis*	*Netta rufina*	*Regulus ignicapillus* (PM)	
Sturnus vulgaris	*Locustella lusciniodes* (O)	*Numenicus arquata*	*Saxicola torquata*	
Sylvia cantillans (PM)	*Lullula arborea* (PM)	*Passer montanus*	*Sylvia borin*	
Sylvia communis (PM)	*Luscinia luscinia*	*Philomachus pugnax*	*Sylvia curruca*	
Sylvia melanocephala	*Luscinia svecica* (PM)	*Phoenicurus ochruros*	*Sylvia deserticola*	
Turdus pilaris (R)	*Miliaria calandra* (PM)	*Plefadis falcinellus* (PM)	*Sylvia hortensis*	
	Milvus milvus	*Podiceps cristatus* (PM)	*Sylvia rueppelli*	
	Motacilla alba	*Podiceps nigricollis*	*Tachymarptis melba*	
	Motacilla flava	*Recurvirostra avosetta*	*Tadorna tadorna* (PM)	
	Oenanthe oenanthe	*Sterna albifrons*	*Tringa erythropus*	
	Oenanthe pleschanka	*Sterna caspia*	*Tringa nebularia*	
	Pandion haliaetus	*Sterna hirundo*		
	Pernis apivorus	*Sylvia artricapilla*		
	Phoenicurus phoenicurus	*Sylvia nisoria*		
	Phylloscopus bonelli (PM)	*Sylvia sarda*		
	Phylloscopus collybita	*Tadorna ferruginea* (PM)		
	Phylloscopus sibilatrix	*Tringa glareola*		
	Phylloscopus trochilus (R)	*Upupa epos* (PM)		
	Platalea leucorodia (PM)	*Vanellus vanellus* (PM)		
	Porzana porzana (O)	*Xenus cinereus*		
	Porzana pusilla			
	Prunella modularis (R)			
	Rallus aquaticus (O)			
	Riparia riparia			
	Saxicola ruberta			
	Scolopax rusticola			
	Serinus serinus (PM)			

Table 5.3 continued

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
	Sylvia conspicillata (PM)			
	Sylvia melanothorax (O)			
	Sylvia nana			
	Sylvia undata			
	Tringa ochropus			
	Tringa stagnatilis			
	Tringa totanus			
	Troglodytes troglodytes (PM)			
	Turdus iliacus (R)			
	Turdus merula (PM)			
	Turdus philomelos (PM)			
	Turdus viscivorus			

Table 5.4: Species in each vulnerability (VU) category according to their vulnerability scores (V) for 2055 A1B scenario**.** Most contributing indicator (R: relative range extent, O: overlap, PM: proportional change in migratory distance) , indicator with a difference of either 3 or more from other indicators, listed next to relevant species.

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: high VU	V26-V30: extremely VU
Acrocephalus arundinaceus (PM)	*Acrocephalus schoenobaenus* (R)	*Accipiter nisus* (PM)	*Anas crecca*	*Acrocephalus scirpaceus*
Alauda arvensis	*Actitis hypoleucos* (R)	*Acrocephalus paludicola*	*Anthus cervinus*	*Anas penelope*
Anas querquedula	*Anthropoides virgo*	*Acrocephalus palustris*	*Apus apus*	*Apus affinis*
Ardea cinerea	*Anthus campestris*	*Anas acuta*	*Aquila nipalensis*	*Bubulcus ibis*
Burhinus oedicnemus (PM)	*Anthus pratensis*	*Anas clypeata* (PM)	*Botaurus stellaris*	*Caprimulgus ruficollis*
Cercotrichas galactotes	*Anthus trivialis*	*Anas platyrhynchos* (PM)	*Calidris alpina* (PM)	*Carpospiza brachydactyla*
Charadrius alexandrinus (O)	*Ardea purpurea* (PM)	*Anthus spinoletta*	*Calidris minuta*	*Charadrius morinellus*
Circus aeruginosus	*Ardeola ralloides* (PM)	*Apus pallidus*	*Calidris temminckii*	*Chlidonais hybridus*
Clamator glandarius (PM)	*Asio flammeus*	*Aquila clanga*	*Charadrius hiaticula*	*Egretta alba*
Coccothraustes coccothraustes	*Asio otus* (PM)	*Aquila heliaca*	*Ciconia ciconia*	*Emberiza caesia*
Columba palumbus	*Aythya nyroca* (PM)	*Aquila pomarina*	*Ciconia nigra*	*Lymnocryptes minimus*
Coturnix coturnix	*Buteo buteo*	*Arenaria interpres*	*Circus macrourus*	*Melanocorypha bimaculata*
Cuculus canorus	*Buteo rufinus* (PM)	*Aythya ferina (PM)*	*Emberiza cineracea*	*Neophron percnopterus*
Delichon urbica	*Calandrella brachydactyla* (PM)	*Aythya fuligula*	*Falco cherrug*	*Oenanthe xanthoprymna*
Emberiza schoeniclus	*Carduelis cannabina* (PM)	*Caprimulgus europaeus*	*Falco columbarius*	*Pelecanus onocrotatus*

Table 5.4continued

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
Erithacus rubecula (R)	*Carduelis carduelis (PM)*	*Egretta garzetta*	*Falco vespertinus*	*Porzana parva*
Fringilla coelebs	*Carduelis chloris (PM)*	*Embeiza cia (PM)*	*Ficedula semitorquata*	*Sterna sandvicensis*
Glareola praticola	*Cettia cetti (PM)*	*Emberiza hortulana*	*Gallinago gallinago*	*Tachybaptus ruficollis*
Gyps fulvus	*Charadrius dubius* (PM)	*Falco eleonorae*	*Gelochelidon nilotica*	
Himantopus himantopus	*Childonias niger*	*Falco subbuteo*	*Geronticus ermita*	
Hippolais languidae	*Chlidonias leucopterus*	*Ficedula albicollis*	*Grus grus*	
Hippolais pallida (PM)	*Cicaetus gallicus* (PM)	*Ficedula hypoleuca*	*Hippolais icterina*	
Lanius senator (PM)	*Circus cyaneus*	*Gallinago media*	*Irania gutturalis*	
Larus genei (O)	*Circus pygargus*	*Hieraaetus pennatus*	*Lanius nubicus*	
Marmaronetta angustirostris (O)	*Coracias garrulus*	*Jynx torquilla*	*Larus fuscus*	
Oenanthe hispanica	*Crex crex*	*Lanius collurio*	*Larus ribundus*	
Oenanthe isabellina (PM)	*Falco naumanni*	*Limosa limosa*	*Limicola falcinellus*	
Sturnus vulgaris	*Falco peregrinus*	*Locustella fluviatilis*	*Limosa lapponica*	
Sylvia communis (PM)	*Falco tinnunculus*	*Locustella lusciniodes*	*Locustella naevia* (O)	
Sylvia melanocephala	*Gallinula chloropus*	*Luscinia luscinia*	*Merops apiaster*	
Turdus merula	*Hippolais polyglotta* (PM)	*Monticola saxatilis*	*Milvus migrans*	
	Hirundo daurica	*Motacilla cinerea* (PM)	*Numenicus phaeopus*	
	Hirundo rupestris	*Muscicapa striata*	*Oriolus oriolus*	
	Hirundo rustica	*Netta rufina*	*Otus scops*	
	Ixobrychus minutus (PM)	*Numenicus arquata*	*Podiceps nigricollis*	
	Lanius minor (O)	*Pandion haliaetus* (R)	*Porzana pusilla*	
	Lullula arborea	*Passer hispaniolensis*	*Saxicola torquata*	
	Luscina megarhynchos (PM)	*Passer montanus* (PM)	*Sterna caspia*	
	Luscinia svecica	*Philomachus pugnax* (R)	*Sylvia borin*	
	Melanocorypha calandra (PM)	*Pluvialis apricaria*	*Sylvia deserticola*	
	Miliaria calandra (PM)	*Regulus ignicapillus* (PM)	*Sylvia rueppelli*	
	Milvus milvus	*Sterna albifrons* (O)	*Sylvia sarda*	
	Monticola solitarius	*Sterna hirundo*	*Tachymarptis melba*	
	Motacilla alba	*Sylvia conspicillata* (PM)	*Tadorna tadorna* (PM)	
	Motacilla flava	*Sylvia curruca*	*Tringa erythropus*	

Table 5.4. continued

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
	Nycticorax nycticorax (PM)	*Sylvia hortensis* (PM)	*Tringa nebularia*	
	Oenanthe oenanthe	*Sylvia nisoria*	*Turdus torquatus*	
	Oenanthe pleschanka	*Tadorna ferruginea* (PM)		
	Pernis apivorus	*Tringa glareola* (R)		
	Phoenicurus ochruros	*Upupa epos* (PM)		
	Phoenicurus phoenicurus	*Vanellus vanellus*		
	Phylloscopus bonelli (PM)	*Xenus cinereus*		
	Phylloscopus collybita			
	Phylloscopus sibilatrix			
	Phylloscopus trochilus			
	Platalea leucorodia (PM)			
	Plefadis falcinellus			
	Podiceps cristatus			
	Porzana porzana (O)			
	Prunella modularis (R)			
	Rallus aquaticus			
	Recurvirostra avosetta			
	Regulus regulus			
	Riparia riparia			
	Saxicola ruberta			
	Scolopax rusticola			
	Serinus serinus			
	Streptopelia turtur (PM)			
	Sylvia artricapilla			
	Sylvia cantillans (PM)			
	Sylvia melanothorax (O)			
	Sylvia nana			
	Sylvia undata			
	Tringa ochropus			
	Tringa stagnatilis			

Table 5.4. continued

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
	Tringa totanus			
	Troglodytes troglodytes			
	Turdus iliacus (R)			
	Turdus philomelos			
	Turdus pilaris (R)			
	Turdus viscivorus (R)			

Table 5.5: Species in each vulnerability (VU) category according to their vulnerability scores (V) for 2085 A1B scenario**.** Most contributing indicator (R: relative range extent, O: overlap, PM: proportion migratory distance) , indicator with a difference of either 3 or more from other indicators, listed next to relevant species.

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
Acrocephalus arundinaceus	*Acrocephalus schoenobaenus*	*Accipiter nisus* (PM)	*Anas acuta*	*Anthus cervinus*
Alauda arvensis	*Actitis hypoleucos*	*Acrocephalus paludicola*	*Anas crecca*	*Calidris minuta*
Ardea cinerea	*Anas querquedula*	*Acrocephalus palustris*	*Anas penelope* (R)	*Calidris temminckii*
Cercotrichas galactotes	*Anthus campestris* (PM)	*Acrocephalus scirpaceus*	*Apus affinis*	*Caprimulgus ruficollis*
Charadrius alexandrinus (O)	*Anthus pratensis* (R)	*Anas clypeata*	*Apus apus*	*Chlidonais hybridus*
Circus aeruginosus	*Anthus trivialis* (R)	*Anas platyrhynchos*	*Bubulcus ibis*	*Lymnocryptes minimus*
Coccothraustes coccothraustes	*Ardea purpurea* (PM)	*Anthropoides virgo*	*Calidris alpina*	*Melanocorypha bimaculata*
Columba palumbus	*Ardeola ralloides* (PM)	*Anthus spinoletta*	*Carpospiza brachydactyla*	*Porzana parva*
Coturnix coturnix	*Asio flammeus* (R)	*Apus pallidus*	*Charadrius morinellus*	*Sterna caspia*
Cuculus canorus	*Asio otus* (PM)	*Aquila clanga*	*Ciconia nigra*	*Sterna sandvicensis*
Delichon urbica	*Aythya fuligula* (R)	*Aquila heliaca*	*Circus macrourus*	*Sylvia sarda*
Erithacus rubecula (R)	*Aythya nyroca* (PM)	*Aquila nipalensis* (O)	*Egretta alba*	
Falco tinnunculus (R)	*Burhinus oedicnemus* (PM)	*Aquila pomarina*	*Emberiza caesia*	
Fringilla coelebs	*Buteo buteo*	*Arenaria interpres*	*Emberiza cineracea*	
Glareola praticola (O)	*Buteo rufinus* (PM)	*Aythya ferina*	*Emberiza hortulana*	
Gyps fulvus	*Calandrella brachydactyla* (PM)	*Botaurus stellaris*	*Falco cherrug*	
Himantopus himantopus	*Carduelis cannabina* (PM)	*Caprimulgus europaeus*	*Falco columbarius*	
Hippolais pallida (PM)	*Carduelis carduelis* (PM)	*Charadrius hiaticula* (R)	*Falco eleonorae*	
Luscinia svecica	*Carduelis chloris* (PM)	*Chlidonias leucopterus*	*Falco vespertinus*	
Marmaronetta angustirostris (O)	*Cettia cetti*	*Ciconia ciconia*	*Ficedula albicollis*	
Oenanthe hispanica (PM)	*Charadrius dubius* (PM)	*Circus cyaneus*	*Ficedula semitorquata*	
Oenanthe isabellina	*Childonias niger* (O)	*Coracias garrulus*	*Gelochelidon nilotica*	
Pernis apivorus	*Cicaetus gallicus* (PM)	*Falco peregrinus*	*Geronticus ermita*	

Table 5.5. continued

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
Phoenicurus ochruros	*Circus pygargus*	*Falco subbuteo*	*Grus grus*	
Riparia riparia	*Clamator glandarius* (PM)	*Ficedula hypoleuca*	*Irania gutturalis*	
Sterna albifrons (O)	*Crex crex*	*Gallinago gallinago*	*Lanius nubicus*	
Streptopelia turtur (PM)	*Egretta garzetta* (PM)	*Gallinago media*	*Limicola falcinellus*	
Sturnus vulgaris	*Embeiza cia*	*Hieraaetus pennatus*	*Limosa lapponica*	
Sylvia communis (PM)	*Emberiza schoeniclus*	*Hippolais icterina*	*Locustella naevia*	
Turdus merula (R)	*Falco naumanni*	*Hippolais polyglotta* (PM)	*Luscinia luscinia*	
	Gallinula chloropus	*Hirundo rupestris*	*Merops apiaster*	
	Hippolais languidae	*Lanius collurio*	*Numenicus phaeopus*	
	Hirundo daurica	*Larus ribundus*	*Oenanthe xanthoprymna*	
	Hirundo rustica (R)	*Locustella fluviatilis*	*Pelecanus onocrotatus*	
	Ixobrychus minutus (PM)	*Locustella lusciniodes*	*Philomachus pugnax* (R)	
	Jynx torquilla	*Milvus migrans*	*Podiceps nigricollis*	
	Lanius minor (O)	*Milvus milvus*	*Porzana pusilla*	
	Lanius senator (PM)	*Monticola saxatilis*	*Sterna hirundo*	
	Larus fuscus	*Motacilla cinerea* (PM)	*Sylvia curruca*	
	Larus genei (O)	*Muscicapa striata*	*Sylvia deserticola*	
	Limosa limosa (O)	*Neophron percnopterus* (PM)	*Sylvia rueppelli*	
	Lullula arborea	*Netta rufina* (O)	*Tachybaptus ruficollis* (PM)	
	Luscina megarhynchos (PM)	*Numenicus arquata*	*Tachymarptis melba*	
	Melanocorypha calandra (PM)	*Oriolus oriolus*	*Tadorna tadorna*	
	Miliaria calandra (PM)	*Otus scops*	*Tringa erythropus*	
	Monticola solitarius	*Pandion haliaetus* (E)	*Tringa nebularia*	
	Motacilla alba	*Passer hispaniolensis*		
	Motacilla flava	*Passer montanus* (PM)		
	Nycticorax nycticorax (PM)	*Phylloscopus bonelli*		
	Oenanthe oenanthe	*Phylloscopus trochilus* (R)		
	Oenanthe pleschanka	*Pluvialis apricaria*		
	Phoenicurus phoenicurus	*Recurvirostra avosetta* (O)		
	Phylloscopus collybita	*Regulus ignicapillus* (PM)		
	Phylloscopus sibilatrix	*Regulus regulus*		
	Platalea leucorodia (PM)	*Saxicola torquata*		
	Plefadis falcinellus (PM)	*Sylvia borin* (R)		
	Podiceps cristatus	*Sylvia cantillans* (PM)		

Table 5.5. continued

V3-V10: least VU	V11-V15: moderately VU	V16-V20: VU	V21-V25: highly VU	V26-V30: extremely VU
	Porzana porzana	*Sylvia conspicillata* (PM)		
	Prunella modularis	*Sylvia hortensis*		
	Rallus aquaticus	*Sylvia nisoria*		
	Saxicola ruberta	*Sylvia undata*		
	Scolopax rusticola	*Tadorna ferruginea* (PM)		
	Serinus serinus	*Tringa glareola* (R)		
	Sylvia artricapilla	*Tringa ochropus* (R)		
	Sylvia melanocephala	*Tringa stagnatilis*		
	Sylvia melanothorax (O)	*Tringa totanus*		
	Sylvia nana	*Turdus torquatus*		
	Troglodytes troglodytes	*Xenus cinereus*		
	Turdus iliacus (R)			
	Turdus philomelos (R)			
	Turdus pilaris (R)			
	Turdus viscivorus (R)			
	Upupa epos (PM)			
	Vanellus vanellus			

Table 5.6: Species IUCN red list category (EN: endangered; VU: vulnerable; NT: near threatened) and their Vscore category (least VU, moderately VU, VU, highly VU and extremely VU) the A1B and A2 emissions scenario and for 3 different time-slices.

Species	IUCN category	A1B Vscore category			A2 Vscore category		
		2025	2055	2085	2025	2055	2085
Falco cherrug	EN	Highly VU	Highly VU	Highly VU	Highly VU	Highly VU	VU
Neophron percnopterus	EN	Extremely VU	Extremely VU	VU	Extremely VU	Extremely VU	VU
Acrocephalus paludicola	VU	Moderately VU	VU	VU	Moderately VU	VU	VU
Aquila clanga	VU	Moderately VU	VU	VU	VU	Highly VU	VU
Aquila heliaca	VU	VU	VU	VU	VU	VU	VU
Falco naumanni	VU	Least VU	Moderately VU	Moderately VU	Least VU	Moderately VU	Moderately VU
Marmaronetta angustirostris	VU	Least VU	Least VU	Least VU	Least VU	Least VU	Least VU
Aythya nyroca	NT	Moderately VU	Moderately VU	Moderately VU	Moderately VU	Moderately VU	Moderately VU
Circus macrourus	NT	VU	Highly VU	Highly VU	VU	Highly VU	Highly VU
Coracias garrulous	NT	Moderately VU	Moderately VU	VU	Moderately VU	Moderately VU	VU
Crex crex	NT	Moderately VU	Moderately VU	Moderately VU	Moderately VU	Moderately VU	Moderately VU
Emberiza cineracea	NT	Highly VU	Highly VU	Highly VU	Highly VU	Highly VU	Highly VU
Falco vespertinus	NT	VU	Highly VU	Highly VU	VU	Highly VU	Highly VU
Ficedula semitorquata	NT	Highly VU	Highly VU	Highly VU	Highly VU	Highly VU	Highly VU
Gallinago media	NT	Moderately VU	VU	VU	Moderately VU	VU	VU
Limosa limosa	NT	VU	VU	Moderately VU	VU	VU	VU
Milvus milvus	NT	Moderately VU	Moderately VU	VU	Moderately VU	Least VU	VU
Numenicus arquata	NT	VU	VU	VU	VU	VU	VU

Species that are extremely vulnerable in all scenarios, such as *Sterna sandvicensis*, are predicted to lose much of their range and have little or no overlap between simulated current and future range (digital appendix). *Acrocephalus scirpaceus* is a species that is classified as extremely vulnerable in 2025 and 2055 but only as vulnerable in 2085. Although the models project a steady decrease in range on the breeding grounds, climatic suitability on the non-breeding grounds improves in 2085 (digital appendix). This species is projected to lose much of its non-breeding range in 2025 and 2055 but increase it in 2085. Contrary to this non-linear temporal response to climate change, other species, like *Sylvia sarda*, are projected steadily to increase their vulnerability score (Tables 5.3-5.5). Many species in the extremely vulnerable category have small ranges (either breeding or non-breeding) which are known to make species more vulnerable to stressors.

Factors affecting species' Vulnerability Scores

Differences in (logged) raw Vscores for species did not differ among future time periods (A1B: $F_{(1.32, 300.97)} = 0.478$, $p = 0.542$; A2: $F_{(1.48, 338.03)} = 0.189$, $p = 0.761$).

No factors affected Vscore in 2025 under either the A1B or the A2 scenario. However, under the A1B scenario, Vscores were affected in the 2055 time-slice by species' habitat ($F_6 = 2.65$, $p = 0.018$), migratory category ($F_2 = 3.54$, $p = 0.031$) and the interaction between habitat and winter biome ($F_{17} = 1.78$, $p = 0.034$). Species inhabiting predominantly coastal or upland environments (Figure 5.2) had significantly greater Vscores than those inhabiting open habitat or forests. Trans-Saharan migrants (Figure 5.3) had significantly greater Vscores than European migrants. *Post hoc* tests also revealed that species in tropical/subtropical grassland, savannah and scrubland or desert and xeric scrubland were significantly more vulnerable than those in temperate broadleaf and mixed forests.

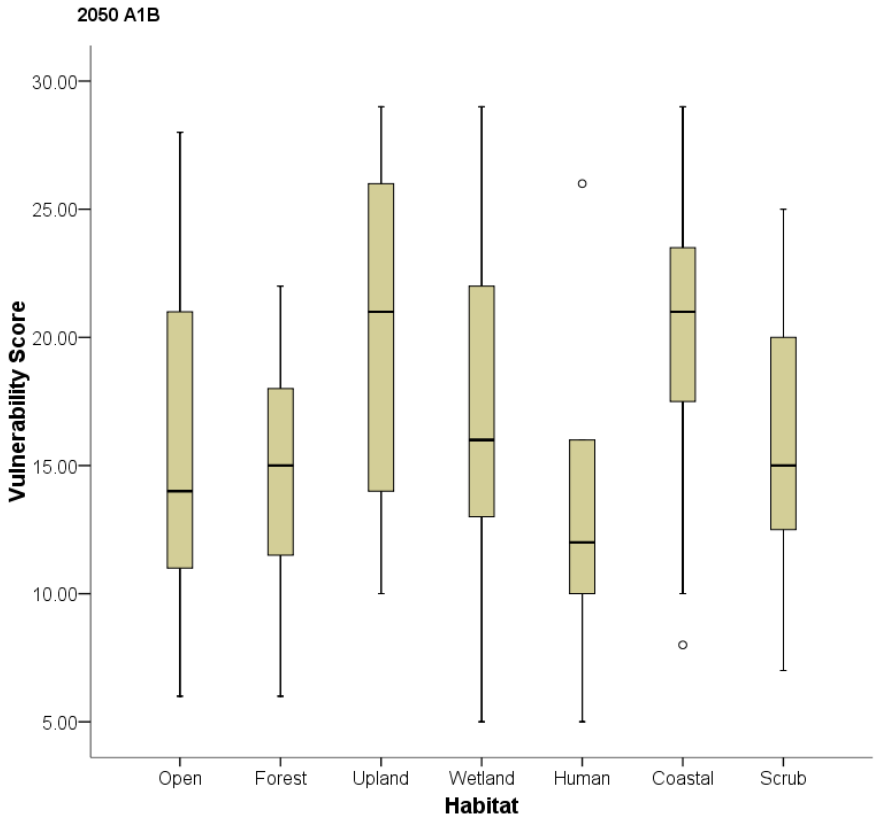


Figure 5.2: Box plots of species' vulnerability score by species' habitat for 2055 A1B scenario. Numbers of species in each category: Open = 59; Forest=52; Upland = 14; Wetland = 52; Human = 5; Coastal = 23; Scrub = 24.

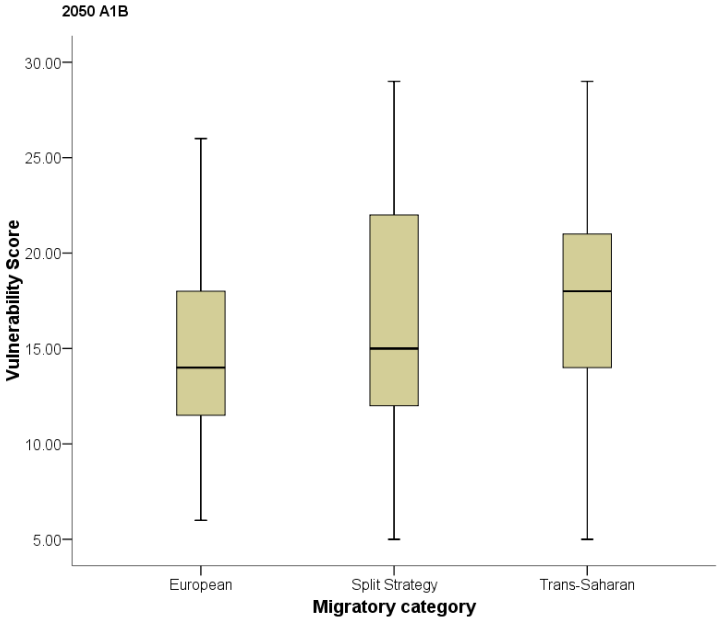


Figure 5.3: Box plots of species' vulnerability score by species' migratory category for 2055 A1B scenario. Numbers of species in each category (see section 4.3)

Under the A1B scenario, Vscores were affected in the 2085 time-slice by species' habitat ($F_6 = 2.39$, $p = 0.031$), migratory category ($F_2 = 5.01$, $p = 0.008$), the interaction between habitat and non-breeding biome ($F_{17} = 2.161$, $p = 0.007$) and the interaction between non-breeding biome and non-breeding tolerance ($F_2 = 4.51$, $p = 0.012$). Species found predominantly in coastal or upland environments (Figure 5.4) had significantly greater Vscores than those inhabiting forests or human environments. Trans-Saharan migrants (Figure 5.5) had significantly greater Vscores than European and Split-strategy migrants. *Post hoc* tests also revealed that species in desert and xeric scrubland were significantly more vulnerable than those in temperate broadleaf and mixed forests.

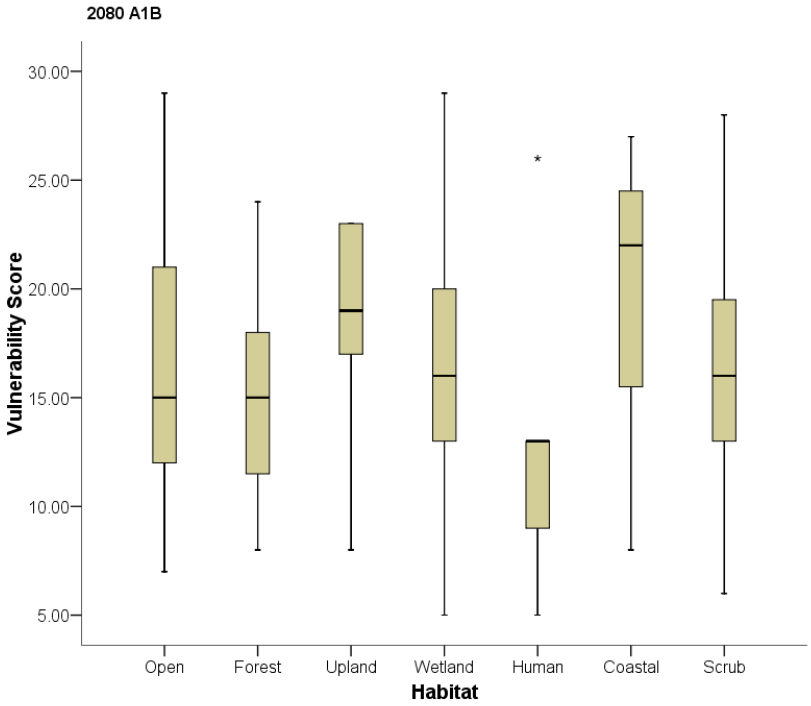


Figure 5.4: Box plots of species' vulnerability score by species' habitat for 2085 A1B scenario. Numbers of species in each category: Open = 59; Forest=52; Upland = 14; Wetland = 52; Human = 5; Coastal = 23; Scrub = 24.

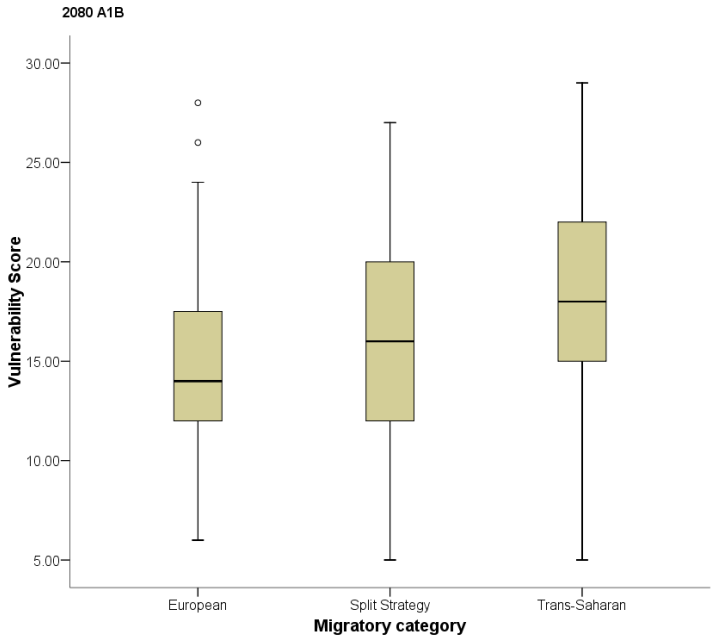


Figure 5.5: Box plots of species' vulnerability score by species' migratory category for 2085 A1B scenario. Numbers of species in each category (see section 4.3)

Under the A2 scenario, Vscores were affected in the 2055 scenario by species' migratory category (F_2 = 3.11, p = 0.047) and the interaction between non-breeding biome and non-breeding tolerance (F_2 = 3.26, p = 0.041). Trans-Saharan migrants were significantly more vulnerable than European migrants (Figure 5.6) while those species in tropical/subtropical grassland, savannah and scrubland were more vulnerable that those in temperate broadleaf and mixed forests.

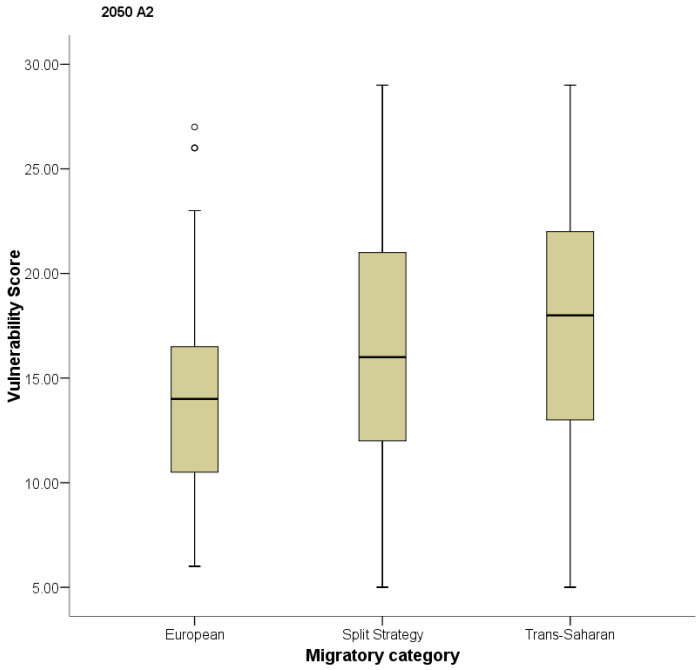


Figure 5.6: Box plots of species' vulnerability score by species' migratory category for 2055 A2 scenario. Numbers of species in each category (see section 4.3)

Under the A2 scenario, Vscores were affected in the 2085 time-slice by species' habitat (F_6 = 2.40, p = 0.030), migratory category (F_2 = 5.49, p = 0.005) and the interaction between habitat and non-breeding biome (F_{17} = 1.86, p = 0.025). Species inhabiting predominantly coastal areas (Figure 5.7) had significantly greater Vscores than those associated with open habitat, forest or human habitat. Trans-Saharan migrants (Figure 5.8) had significantly greater Vscores than European and Split-strategy migrants. *Post hoc* tests also revealed that species in desert and xeric scrubland were significantly more vulnerable than those in temperate broadleaf and mixed forests.

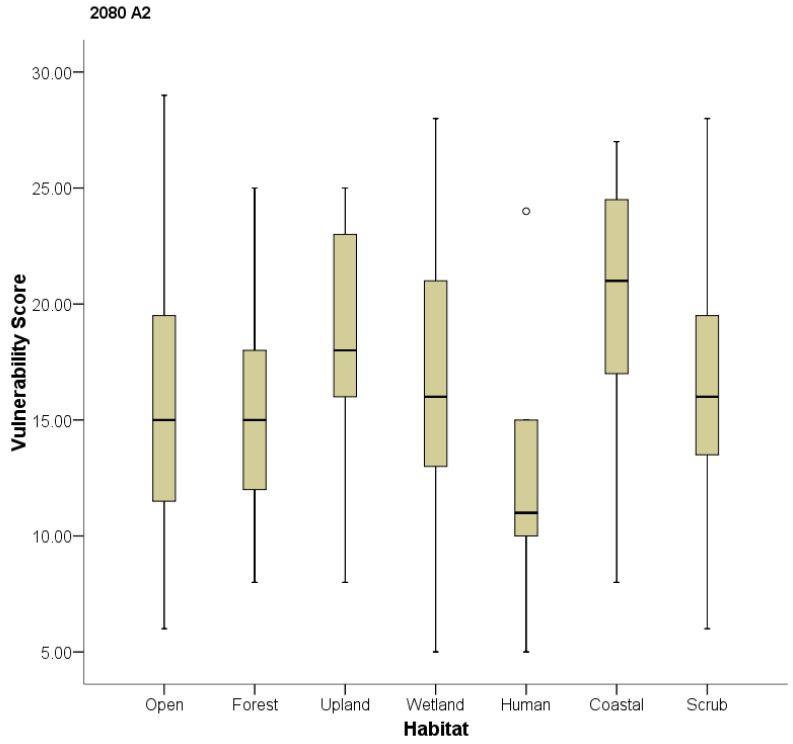


Figure 5.7: Box plots of species' vulnerability score by species' habitat for 2085 A2 scenario. Numbers of species in each category: Open = 59; Forest=52; Upland = 14; Wetland = 52; Human = 5; Coastal = 23; Scrub = 24.

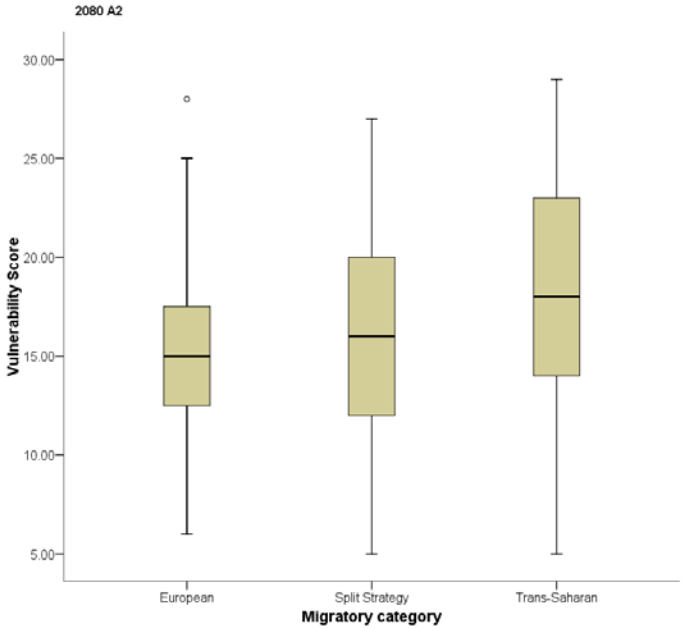


Figure 5.8: Box plots of species' vulnerability score by species' migratory category for 2085 A1B scenario. Numbers of species in each category (see section 4.3)

IUCN Red list and Vscores

Table 5.6 (p.208) shows species' red list categories and their Vscores. Most species' climate sensitivity increases through time. The A2 scenario projects virtually the same classification as the A1B scenario.

Falco cherrug and *Neophron percnopterus* are currently classified as endangered and are at a very high risk of extinction. *Falco cherrug* is classified as EN mainly because of the falconary trade, habitat degradation and pesticides (Birdlife International, 2004). *Neophron percnopterus* is classified as EN with severe declines in India, Europe and Africa (Birdlife International, 2004). Both these species are also projected to suffer from the impact of climate change. *Falco cherrug* is classified as highly vulnerable in all time periods. *Neophron percnopterus* is classified as extremely vulnerable for 2025 and 2055, but only as vulnerable for 2085, although it is likely that sustained pressure from the first part of the century may inhibit recovery in the more favourable conditions predicted in the latter part of the century.

In the IUCN VU category, three of the five species are classified as either moderately vulnerable to climate change or vulnerable to climate change. *Falco naumanni* is classified as least vulnerable in 2025, however, and *Marmaronetta angustirostris* as least vulnerable in all time periods. *Marmaronetta angustirostris'* populations have declined throughout their winter range due to extensive habitat destruction (Birdlife International, 2004). Habitat was not taken into account in the modelling process so it may be that the climate model projections are not enough to project species' true climate sensitivity because climatic change may interact with habitat change. *Falco naumanni* is also declining due to habitat loss (Birdlife International, 2004).

In the IUCN NT category, the majority of species are categorised as either moderately VU or VU. *Falco vespertinus* and *Circus macrourus* are classified as highly VU from 2055 onwards and *Ficedula semitorquata* and *Emberiza cineracea* as highly VU in all time periods. Habitat loss and degradation are thought to be contributing to decline of these species' populations (Birdlife International, 2004). These species' climate sensitivities are such that the IUCN categorisation may require upgrading if species' populations further decline due to climate change. Akçakaya *et al.* (2006) suggest that species could be upgraded to VU (but not EN or CR) due to climate change threat under criterion D (defined as "Population with a very restricted area of occupancy (typically less than 20 km^2) or number of locations (typically five or fewer) such

that it is prone to the effects of human activities or stochastic events within a very short time period in an uncertain future", p.23) of the Red list criteria (IUCN, 2001).

Only 19 migratory birds are currently listed as threatened or near threatened. The vulnerability index however, shows that some species (Tables 5.3-5.5) are likely to be severely affected by climate change and may need to be classified as NT until the relevant conditions are met for species to be listed as threatened on the Red list (Akçakaya *et al.*, 2006).

5.1.4 Discussion

The results suggest that 6% of the migrant bird species analysed are extremely vulnerable to climate change and that a further 20% are highly vulnerable. These migrants are projected to lose much of their current range without new range becoming available on either their breeding or non-breeding grounds, along with a lengthening of their average migratory distance. Most of the species that are extremely vulnerable to climate change are non-passerine species with narrow ranges. Many of these species will also be dependent on particular habitat requirements that may be further degraded by climate change impacts. The results presented are continent-wide. However, species may be regionally exposed to different conditions and so their response may be more plastic than projected (Laidre *et al.*, 2008). On the other hand, the results may be conservative, because measures from only one of the seasonal ranges are used. Moreover, as Harte *et al.* (2004) suggest, evolutionary adaptation may make species less vulnerable than previously thought, with responses being mediated through ecological, physiological and population dynamic processes. Indeed Thomas *et al*. (2001) showed plastic responses to climate change by four insect species, with two species increasing the variety of habitats they could colonise and two species increasing the number of dispersive phenotypes so as to colonise newly suitable areas. However, insects have rapid population turnover and high numbers which facilitates rapid selection. This may not be the case for bird species. Moreover, under the precautionary principle, it has to be assumed that species may not be able to adapt.

The results also revealed differential changes in species' vulnerability through time. Some species' vulnerability is projected to change linearly whilst other species exhibited a non-linear response. This non-linear response, often seen as amelioration in conditions towards the end of the century, can be technically explained by the movement of a species' climatic envelope through time across the fragmented space that makes up the study area. The space is fragmented

because the underlying climate, upon which the climate models are built, fit a global space, whilst the species distribution models fit a restricted space. The effects of non-linearity in future climatic suitability may be evidenced through population fluctuations. Amelioration in climatic suitability for some species towards the end of the century may provide a mechanism for species' survival. Indeed, change in climatic suitability is unlikely to impact species instantaneously. In a recent study, Devictor *et al.* (2008) showed that birds were lagging behind climate change.

Currently, the majority of European birds are not listed as threatened on the IUCN Red list. IUCN are looking at ways to incorporate future climate change impacts into their decision criteria but have not done so yet because "the understanding of the response of any specific species to future climate change is not sufficiently robust to provide quantitative estimates"[2] (Parmesan and Hilton-Taylor, 2005). However, a handful of studies have tried to do so. Thomas *et al.* (2004) used changes in range extent as a proxy for extinction risk and found that 5-16% species were projected to lose all range by 2050 and 15-40% to lose 90% of their range by that date (Thomas *et al.*, 2004). Loosely using the IUCN criteria, Bomhard *et al*. (2005) calculated the current threat status of Proteaceae taxa in the Cape Floristic region and then calculated the future threat status using future overlap range extents for 2020 climate change and land-use change scenarios. They concluded that, although the threat category of the majority of the study taxa did not change in the future, between 3.5% and 29.1% of taxa would be uplisted, and 1.7% of taxa would be down listed. My results also indicate some amelioration in vulnerability status to climate change for some species. However, amelioration in climate space may or may not translate to population changes.

Thuiller *et al*. (2005b) evaluated future extinction risk from climate change for 1350 plant species in Europe for 2065, using a combination of range loss, overlap and new range. Under a no migration scenario, their results indicated that over 50% of species would be classified as VU or above, whilst under the full migration scenario about 30% of species would fall into a threatened category. Thuiller *et al.'s* (2005b) study was criticised by IUCN in a press release (Parmesan and Hilton-Taylor, 2005) whilst all the above mentioned studies were criticised in a paper by Akçakaya *et al.* (2006). Akçakaya *et al.* (2006) argue that all these studies misapplied the IUCN criteria, that have stringent rules (Rodrigues *et al.*, 2006), and hence introduce bias and uncertainty. Specifically, Akçakaya *et al.* (2006) find five areas of fault. First of all, quantitative estimates of extinction risk can only be obtained if enough data, such as demographic data, are

[2] http://intranet.iucn.org/webfiles/doc/SSC/SSCwebsite/News/Climate_change_editorial.pdf

available. Second, the IUCN criteria have a clear temporal scale of 10 years or 3 generations. All the studies used different time-scales that do not match the criteria. Third, is the issue of spatial scale. The IUCN Red List is made from a global assessment, to take into account species' entire range. All the studies concentrate on only part of species' ranges such as Europe in Thuiller *et al.*'s (2005) study. My results, for the most part, take species' entire range into account. However, this is not the case for some species. For example, *Neophron percnopterus* also resides in India which was not modelled. Fourth, is the question of resolution and spatial measures. My study like many studies on climate change impact is of too coarse a resolution accurately to portray extinction risk. The IUCN uses two spatial measures: extent of occurrence and area of occupancy. My study like many others only examines extent of occurrence which does not necessarily equate to area of occupancy. Moreover, changes in population size can occur at a faster rate than changes in range extent (Shoo *et al.*, 2005b) and rate of change in occupancy can also accelerate with reduced range size (Rhodes *et al.*, 2008). Fifth, climate change impact studies often assume that the relationship between distribution and population size is linear. Although this is sometimes the case, it is not always valid, and nor will species decline at the same rate that area declines (Akçakaya *et al.*, 2006). Because of all these factors, using climate impact modelling studies to estimate extinction risk is difficult. However, Akçakaya *et al.* (2006) suggest that they might be used to classify species currently not at risk as NT or potentially as VU using criterion D (IUCN, 2001; IUCN, 2006). Because of all these difficulties, this study has not attempted to estimate species' extinction risk but, rather, to highlight species' vulnerability to climate change and explore whether species currently on the Red List index are also vulnerable to climate change. This study finds that many species projected to be the most vulnerable to climate change are not currently on the Red List and may therefore need to be monitored. Furthermore, those already on the red list are mostly sensitive to future climate change.

Factors affecting species' sensitivity to climate change

Many studies have sought to find correlates of "extinction risk" or any ecological traits that might predispose species to changes in range as a result of environmental modification. Sekercioglu (2007) analysed extinction risk of birds in the Amazon from fragmentation. He found that specialist bird species were more vulnerable than generalists to habitat modifications, even if they were mobile. Thuiller *et al*. (2005a) analysed whether species' niche properties or niche extent were related to species' sensitivity to projected climate change. They found that some niche

characteristics contributed to sensitivity but that exposure to climate change was the determining factor. They concluded that niche characteristics were powerful indicators of sensitivity. Specifically they found that boreo-alpine species were highly sensitive while Mediterranean species with medium niche breath and size were not, as they potentially benefited from climatic change. My study found that overall vulnerability of migratory species, as defined by range loss, little overlap and increasing migratory distance, was greatest among species from dry environments. However, like Thuiller *et al*. (2005), who used only range extent, boreo-alpine species were projected to have reduced range sizes in the future.

Two previous studies examined the ecological and life-history traits that might be correlated with observed range changes. Amano and Yamaura (2007) used a phylogenetic generalised least squares model and an ordinary least squares model to find the traits that were associated with the contracting ranges of breeding birds in Japan. Both models found that species with medium body-size, low annual productivity, solitary breeding, farmland habitat and long-distance migrants all experienced severe range contractions. The similar results obtained from their two models showed that "comparative data were not so dependent on phylogeny" (Amano and Yamaura, 2007, p.278). Jetz *et al.* (2008) also found phylogeny to be of negligible importance in the analyses of their comparative data. These findings give greater confidence in my results that do not attempt to include such comparative analyses.

Okes *et al.* (2008) examined how habitat use and life history affected water bird responses to habitat change in South Africa. They found that species that had expanded their ranges were mobile species capable of long-distance migration. However, they did not find that any life-history traits predisposed water birds to range change in response to habitat change. An interesting finding of this study was that anthropogenically mediated habitat change was more of an influential driver in range change than climate change. Indeed some bird species responded to the creation and/or destruction of wetlands by expanding or contracting their ranges. Climate change impacts could therefore be mitigated by the creation of species-specific habitats or as a result of certain land-use changes. Indeed it is possible that irrigation in the southern margin of species' ranges is the reason why some predicted contractions of range have not been seen (Böhning-Gaese and Oberrath, 2003).

My results show that species' ecology (habitat, migratory category and biome) affects species' vulnerability to projected climate change. Coastal and upland species are projected to be more vulnerable, as are grassland, savannah and desertic species. Coastal and upland species are more likely to have smaller ranges, constrained by geography. Moreover, these areas are

generally climatically different to the surrounding landscape, making it difficult for species to find contiguous climate space in the future.

The results also show trans-Saharan migrants to be more vulnerable to climate change than European and split strategy migrants. This finding may support the hypothesis put forward in the literature that climate has contributed to the current declines in long-distance migrants (Sanderson *et al.*, 2006; Amano and Yamaura, 2007). However, this interpretation of my results relies on the assumptions of the modelling techniques used (see Chapter 3), which are not always met (see Chapter 3 & 6). Moreover, it assumes that climate is the overarching factor determining species' distributions and population change which may not be true (see section 5.2). Finally it is likely that other factors, such as habitat loss, have also played an important role in driving trans-Saharan migrants' population declines. Long-distance migrants may also be more vulnerable than the index calculated here suggests because it takes no account of the changes in phenology that have been reported to be affecting migrants (Both *et al.*, 2006).

The results indicated that niche breadth did not impact on the vulnerability scores. It is often thought that niche breadth should be important in terms of sensitivity to environmental change (Thuiller *et al.*, 2005a; Sekercioglu, 2007). However, Thuiller *et al.* (2005a) also did not find a clear signal that niche breadth affected species' sensitivity to climate change. One of the reasons why this might be the case is that ranges of specialised species with narrow geographic distributions are often overestimated in broad scale atlas data (Jetz *et al.*, 2008). This would mean that the estimates of species' sensitivity to climate change are over-optimistic.

As well as characterising which species were most vulnerable to the effects of climate change, this study also looked at the relationship between species' ecology and specific measures of change in distribution: changes in range extent, loss of current climate space (overlap), and changes in average migratory distance. The results indicate that forest species are more likely to experience contractions in range extent in the future. Wetland and coastal species are more likely to experience low overlap between current and future suitable climate. Forest and wetland species are more likely to experience greater proportional change in migratory distance in the future.

In terms of biome, which is also a proxy for latitude, forest/taiga species are more likely to experience contractions in range extent, which is a result of pole-ward squeeze of biomes in their European breeding areas. Drier biome species are more likely to experience low overlap between current and future areas of suitable climate; whilst forest, Mediterranean and grassland species are more likely to experience greater proportional change in migratory distance in the future.

5.1.5 Conclusion

The results of this study suggest that trans-Saharan migrants, coastal species, upland species and those currently living in drier biomes are most likely to be vulnerable to the impacts of climatic change. However, uncertainty surrounding these results is still large despite using all the methodology available to reduce the uncertainty, such as testing the robustness of the models, using a consensus model and using a multi-model average.

An important area of uncertainty is how population dynamics and changes in numbers of individuals relate to geographical distribution changes. Although potential range changes are interesting and important for the management of populations, knowledge of how populations might change, or whether they will change, in response to climate change is vital for conservationists. Indeed species may be sensitive to climate change, but population dynamic processes may buffer changes in species' numbers (Ådal *et al.*, 2006). In the next section, changes in climatic suitability, as modelled by the species distribution models used throughout this thesis, will be used to investigate these questions.

5.2 Recent population changes and climate

5.2.1 Introduction

Changes in the number of birds within different countries across Europe have been documented in a number of studies. The most comprehensive Europe-wide studies have been undertaken by the Pan-European Common Bird Monitoring Scheme with data from 1980-2004, and by BirdLife International for the period 1970-1990 (Tucker and Heath, 1994) and the period 1990-2000 (Birdlife International, 2004). These censuses highlight widespread declines of forest and farmland specialists (Gregory *et al.*, 2007), as well as of long-distance migrants (Sanderson *et al.*, 2006).

Various factors have been proposed to explain these declines. Habitat loss and degradation, land-use change and persecution account for the majority of the declines. Indeed the 20th century saw major changes to the European landscape. Much semi-natural habitat has been destroyed since 1945: wetlands were drained and forests, hedgerows and heath lands cleared for intensive agriculture (Fuller and Ausden, 2008; Dallimer *et al.*, 2009). Agricultural intensification caused declines of many species. In the UK, declines in farmland birds coincided with the main period of agricultural intensification between 1970-1988 (Chamberlain *et al.*, 2000; Newton, 2004). Changes in woodland management, especially reduction of coppicing as well as natural succession, were also the cause of some bird population changes (Fuller *et al.*, 2007; Holmes, 2007). By contrast, in the latter part of the 20th century, conservation of bird habitats and the creation of man-made water-bodies, as well as species' protection measures, have resulted in the recovery of some bird populations (Birdlife International, 2004; Bauer *et al.*, 2008; Ausden and Fuller, 2009).

Changes on the African non-breeding grounds may also have contributed to population changes. Agricultural intensification and desertification have impacted on species' non-breeding habitats (Sanderson *et al.*, 2006). Moreover, drought in Sub-Saharan Africa between 1960 and 1990 caused many trans-Saharan bird populations to decline (Peach *et al.*, 1991; Baillie and Peach, 1992; Marchant, 1992; Jones *et al.*, 1996). Clearly, severe climatic and weather-realted changes can have important consequences for bird populations.

Climatic change as a driver of population change

Climatic change has been suggested as a cause of some population declines (Birdlife International, 2004; Beale *et al.*, 2006; Sanderson *et al.*, 2006; Mac Nally *et al.*, 2009). However, "the mechanisms behind how environmental change translates into population change are poorly understood" (Ådahl *et al.*, 2006, p.1627) and the amount climate change contributes to population change is also unknown. Analyses of historical analogues may give some insight into how populations respond to a period of climatic change. Lister and Stuart (2008) analysed the response of large mammals to climate change in the late Quaternary. Following climate-mediated changes to their habitat, large mammals' ranges and abundances contracted which, coupled with human intervention (hunting), ultimately led to species' extinction.

Several studies have sought a direct link (though not a causal link) between population change in birds or some other demographic parameter and climate. Saether *et al.* (2000) showed that variation in reproductive rate in *Cinclus cinclus* populations in southern Norway was influenced by population density and mean winter temperature. Barbraud and Welmerskirsh (2001) showed that annual average sea temperature in the Sourthern Ocean accounted for most of the yearly survival of *Aptenodytes forsteri.* Beale *et al.* (2006) suggest that the decline of *Turdus torquatus* populations in Britain may be due to changes in climate, as the decline in territory occupancy was related to climatic variables, specifically to summer temperature and rainfall and winter rainfall. Finally, MacNally *et al*. (2009) suggest that the collapse of the avifauna of the interior *Eucalyptus* woodlands of South-East Australia may be in part climate driven, as they found no other factor contributing to species' decline in their analysis. The studies mentioned here are a few examples from the literature but are by no means intended to be representative or exhaustive.

Jonzén *et al.* (2002) used population models to analyse changes in migratory populations with winter quarters in Europe. They found that winter climate affected rate of population change of migratory birds. Sillett *et al.* (2000) investigated the effect of El Niño Southern Oscillation on *Dendroica caerulescens* by correlating Southern Oscillation Index (SOI) with annual survival on the breeding and non-breeding range. They found a strong correlation between SOI and annual survival on the non-breeding range but not on the breeding range. However, annual fecundity was also correlated with SOI and affected species' demography in the subsequent year (Sillett *et al.*, 2000). This indicates that climatic change may have time-lagged effects on species' populations. Sandvik *et al.* (2008) also found the presence of time lagged climatic effects on breeding success

in their study of 13 seabirds. Anders and Post (2006) quantified the relationship between climate and population dynamics of *Coccyzus americanus*. They found that macroclimate affected population densities with a one year time lag. Furthermore, their analysis indicated that "the strength of the effect of local temperatures was predictive of long-term population decline" (Anders and Post, 2006, p.226). This indicates that climate impact studies such as this thesis may therefore be useful in determining the effects of climate change on species' populations as well as on their distribution. However, other factors than climate, such as habitat availability, affect species' populations.

Climate envelopes and population change

The use of species' climate envelope models (CEM) to infer future population change or extinction risk has been heavily criticised (see previous section), mainly because the link between range change, which is what CEM project, and species' populations is not necessarily straightforward. However, it is not unreasonable to use changes in climatic suitability as projected by CEM to infer population changes. Indeed, it can be argued that climatic suitability is just as relevant an index to species (if not more, as CEM are tailored to represent species' niches) as SOI or the North Atlantic Oscillation. Green *et al.* (2008) demonstrated this by using trends in climatic suitability as modelled by Climate Response Surfaces to predict past bird population trends (1980-2002) in the UK. They found a positive association between population trends and climatic suitability, although there was considerable unexplained variation in the models. They concluded that these results provided greater confidence in CEM as well as the possibility of using CEM to explore the impacts on populations as well as range changes.

In this study, I will explore which factors, including breeding and non-breeding climatic suitability trends as projected by CEM, contribute to migratory bird population trends during the periods 1970-1990 and 1990-2000. It is expected that habitat may be an important factor for the 1970-1990 period when landscape change was greatest both in Europe (Chamberlain *et al.*, 2000) and Africa (Olson *et al.* 2004). Passerines and non-passerines may also differ in their population trends and in which factors are important, because differences in mean body size may affect, for example, population growth rate and species' vulnerability to threats. Bauer *et al.* (2008) found significant diverging trends in species richness of passerines and non-passerines in central Europe between 1980-1990 and 1990-2000. Non-passerines, on the other hand may be more habitat

dependent as many are wetland or coastal birds. Therefore, the analysis will be done separately for the two taxonomic groups as well as for all species as a group.

5.2.2 Methods

Climate data

Precipitation, temperature and cloudiness data were taken from the CRU TS 2.1 data set (Mitchell and Jones, 2005). This data set comprises monthly values from climate observations from 1901-2002 that are gridded at a global level at 0.5 º longitude x latitude. These variables interpolated to the grids used in the study using spline surfaces (method describe in Hutchinson, 1989) for each year from 1960-2000. These variables, in conjunction with soil texture, were transformed to provide the set of bioclimatic variables as described in Chapter 3.

Population data

Bird population trend data for the 1970-1990 period (Tucker and Heath, 1994) and 1990-2000 period (Birdlife International, 2004) were gathered for each of the 229 species used in this thesis. Data for the 1970-1990 period were scarcer than for 1990-2000. In the first time series, population trends were available for 141 species and, in the second time series, for 205 species. Average European population trends were categorised as large decline, small decline, stable, small increase and large increase for the first time period and as large decline, moderate decline, small decline, stable, small increase, moderate increase and large increase for the second (Tucker and Heath, 1994; BirdLife International, 2004). These were coded on ordinal scales ranging from -2 to +2 for the 1970-90 period and -3 to +3 for the 1990-2000 period. No data values, as well as those categorised as fluctuating populations (nine species in each time period) were coded as missing data and omitted from the analyses.

Models and analyses

Climate Response Surfaces (CRS) and Generalised Additive Models (GAM) were fitted for each species to the climatic norm (see Chapter 3) and then run for each year (1960-2000) for every species for both the breeding and non-breeding grounds.

Species' average climate suitability (probability of occurrences) was calculated separately for the breeding grounds and non-breeding grounds for each year. For each time period, a

regression was performed on logit transformed annual averages. The slope of the regression was termed the climatic suitability trend (CST).

All species

The relationship between GAM and CRS breeding climatic suitability trend (CSTb) and non-breeding climate suitability trend (CSTnb) was tested using Pearson's correlation for the entire time period. Kruskall-Wallis tests were conducted with population trend as the response and habitat, migration category, order, breeding biome and winter biome as the independent variables.

To model the effect of these factors and climate on population trends, a particular class of logistic regression models was used. Because the dependent variable is ordinal, using a model that incorporates the ordinal nature of the variable is necessary. Ordinal regression was developed by McCullough (1980) based on the idea that the response categories are seen as adjacent cut-offs on a continuous scale. The odds of the response falling within a category or lower categories are described by (Eq. 5.1; McCullagh, 1980; Johnson and Albert, 1999):

$$\text{Log}[\gamma_j(x)/(1-\gamma_j(x))] = \theta_j - \beta x \qquad (1 \leq j < k) \qquad (5.1)$$

Where $[\gamma_j(x)/(1-\gamma_j(x))]$ is the odds of getting score j (with k number of categories); x is the given covariate, β is a vector of unknown parameters and θ_j is the cut-off for category j of k.

Equation 5.1 is called the proportional odds model and uses a log link function. Another type of ordinal regression models is the proportional hazards model which uses a complementary log-log link function (Eq. 5.2; McCullagh, 1980):

$$\text{Log}[-\log(1-\gamma_j(x))] = \theta_j - \beta x \qquad (5.2)$$

This model is based on conditional, rather than cumulative, probabilities used in the proportional odds model (Harrell, 2001). The complementary log-log link function is useful if the response variable is skewed (SPSS Inc., 2006). In the proportional odds model, the logit link function assumes the response variable is evenly distributed whilst using a probit link function (ordinal probit model) assumes a normal distribution (SPSS Inc., 2006).

Ordinal regression was performed in R using the *polr* function in the MASS package (R Development Core Team, 2006) with population trend as the response variable and a complementary log-log link function (proportional hazards model). This link function was chosen because the response variable was skewed. Other link functions were also tried but model fit indicated that the complementary log-log link function was indeed better suited.

Twenty-four models in total were run for each time period and Akaike's Information Criterion (AIC) was used to select the best models. The first model was a null model (containing only 1 as the predictor variable). The subsequent models included climate variables (CSTb and CSTnb) as well as significant confounding variables, such as habitat (see Table 3.15), biome (see Fig. 3.5), taxonomic grouping (passerine or non-passerine) or migratory strategy. A step-wise AIC procedure was used to determine the minimum adequate model (MAM). The MAM was termed the 'base model' and contained only the variables that that had been shown (by Kruskal Wallis tests) to significantly affect species' population trends. Stepwise regression procedures have been shown to have several flaws, one of which is the final chosen model – MAM, which is not generally the best model (Johnson and Omland, 2004; Whittigham *et al.*, 2006), and consequently many authors have advised against their use (Whittigham *et al.*, 2006; Mundry & Nunn, 2009). However, the reason for the use of stepwise regression and MAM, in this thesis, was to find a baseline model to control for major effects, an approach which has been recently suggested as an instance where the use of stepwise procedures is appropriate (Garamszegi *et al.*, 2009).

The next group of models included the base model and either CSTb or CSTnb or both (here after called 'climate'). In the following models, CSTb and CSTnb with either a two- year or a one-year time lag were included. Many studies have found a one- or two-year time lag in bird population responses to inter-annual climatic variability (Sillett *et al.*, 2000; Anders and Post, 2006; Thingstad *et al.*, 2006; Sandvik *et al.*, 2008). The final models tested included, as well as the base model, CSTb with one-year time lag and CSTnb with two-year time lag or CSTb and CSTnb with a one-year time lag. Models were built using GAM and CRS climate suitability trends. The final models considered for comparisons were those with a ΔAIC of less than 7 (Burnham and Anderson, 2002). Furthermore, only models better than the null model (smaller ΔAIC) or within 2 ΔAIC of the null model (Burnham and Anderson, 2002) were considered.

GAM and CRS fitted ordinal models were compared using likelihood ratio tests to establish whether the two models were significantly different from each other. Likelihood ratio tests were also used to compare the null model against the base model, and the base model

against the other models. Comparison with the null model tests whether the model without predictors is significantly different from a model with predictors and gives an indication of model fit.

Goodness-of-fit of ordinal regressions is given by the residual deviance and follows a χ^2 distribution. Residual deviance divided by the degrees of freedom gives the over-dispersion of the model (Johnson and Albert, 1999). Analyses of residual deviance (likelihood ratio tests) can be used in model selection like AIC and determines, for example, the fit of the model versus the null model. Both analyses of residual deviance and AIC were used to select the best model(s). To test whether an independent variable had a statistically significant relationship with the dependent variable, the Wald statistic was calculated and compared against the Chi-square distribution (SPSS Inc., 2006). However, both analyses of residual deviance and the Wald test need to be corrected for over-dispersion (see Johnson and Albert, 1999).

Chi-square tests were undertaken to determine goodness-of-fit for each species using the predicted trend values (highest probability) for each species from the models and the observed trend. The predicted trend values for each species were also transformed into 3 trend direction values (sum of decreasing probabilities, stable probabilities, sum of increasing probabilities). Chi-squares tests were then undertaken using observed direction of trend (decrease, stable, or increase) against predicted direction of trend.

Non-passerines and passerines

Kruskall-Wallis tests were conducted for both time periods with population trend as the response and habitat, migration category, order, breeding biome and winter biome as the independent variables for each taxonomic group separately.

For non-passerines, ordinal regression models were built as above with up to a five-year time lag in CST. Thompson and Ollason (2001) showed a five year time lag in *Fulmarus glacialis* population response to environmental change, in terms of summer temperature anomalies and winter NAO index, due to their delayed reproduction. Non-passerines were further split depending on age of first breeding (one-two years; and above two years) before redoing the analyses.

For passerines, ordinal regression models were built as detailed in the 'all species' analysis. 'Base models' were only built if any of the non-climatic variables proved to have an

effect on population trends. Otherwise, models including only the climate suitability trends were built.

5.2.3 Results

Climatic suitability

Climatic suitability varied greatly among years and species (Tables A27-29). Figures 5.9-5.10 show annual variation in mean climatic suitability for *Erithacus rubecula* and *Sylvia atricapilla* respectively. These show that the scatter in climatic variability produces very weak trends. In some cases, as for *Erithacus rubecula,* both GAM and CRS produce similar trend values (in the same direction), but in other cases, such as for *Sylvia atricapilla,* there are subtle differences (GAM and CRS have a different direction of trend for the breeding models). However, correlations between 1960-2000 GAM CST and CRS CST (Fig. 5.11) were significant (Breeding: rho = 0.838, $p<0.0001$; Non-breeding: rho = 0.666, $p<0.0001$) showing that climatic suitability trends were similar for both modelling techniques. Trends were slightly stronger during the 1990-2000 period than for the 1970-90 period (Table 5.7).

Table 5.7: Median, minimum and maximum breeding climatic suitability trends (CSTb) and non-breeding climatic suitability (CSTnb) as modeled by GAM and CRS for two time periods

	1970-1990				1990-2000			
	CSTb		CSTnb		CSTb		CSTnb	
	GAM	CRS	GAM	CRS	GAM	CRS	GAM	CRS
Median	-0.0001	-0.0007	-0.0005	-0.0012	-0.0008	0.0006	0.0012	0.0028
Minimum	-0.0509	-0.0293	-0.0156	-0.0167	-0.0446	-0.0263	-0.0529	-0.0176
Maximum	0.0250	0.0124	0.0055	0.0067	0.0274	0.0489	0.0293	0.0556

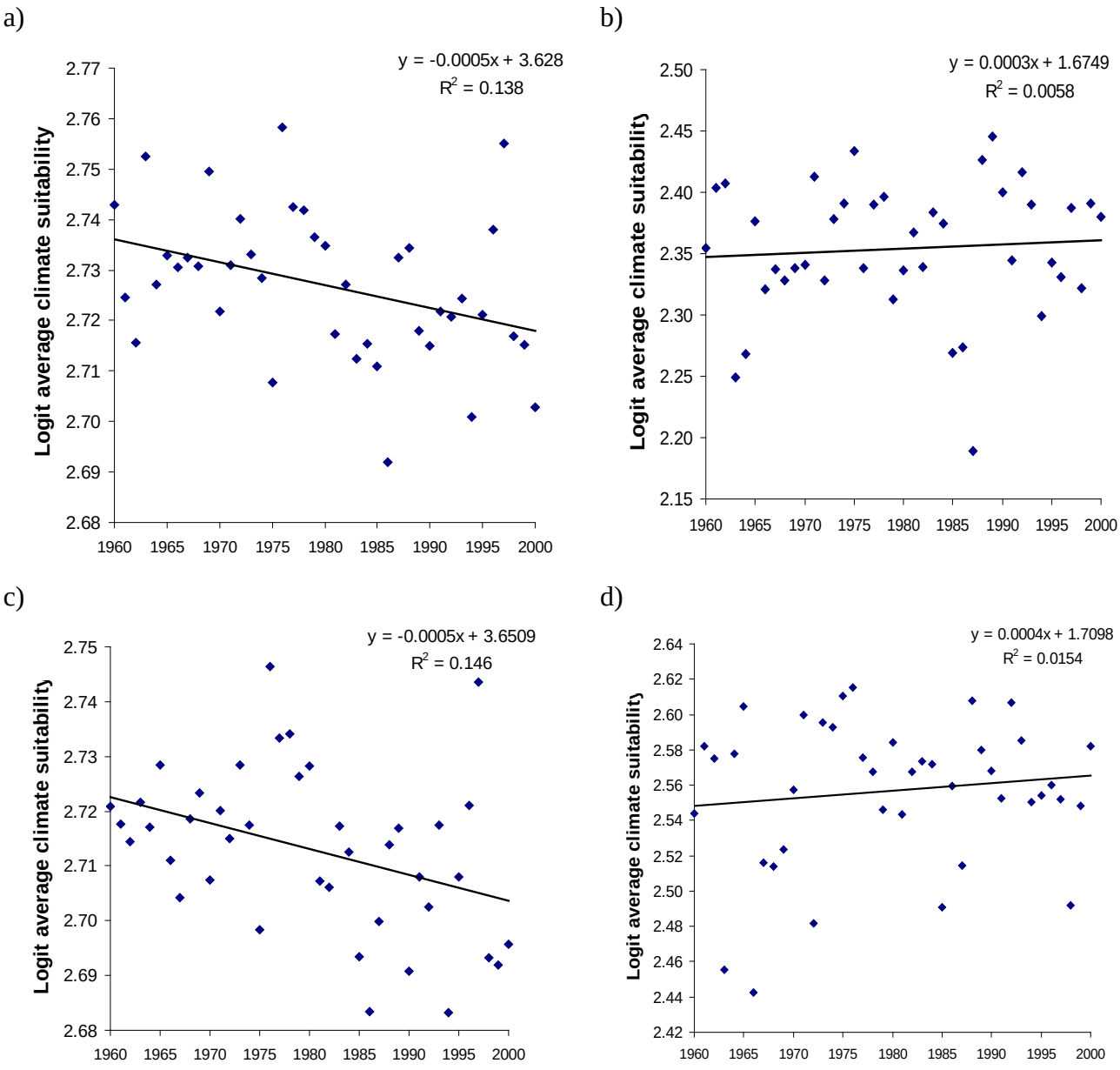


Figure 5.9: Logit average climate suitability and trend for *Erithacus rubecula* for a) GAM breeding model, b) GAM non-breeding model, c) CRS breeding models and d) CRS non-breeding model

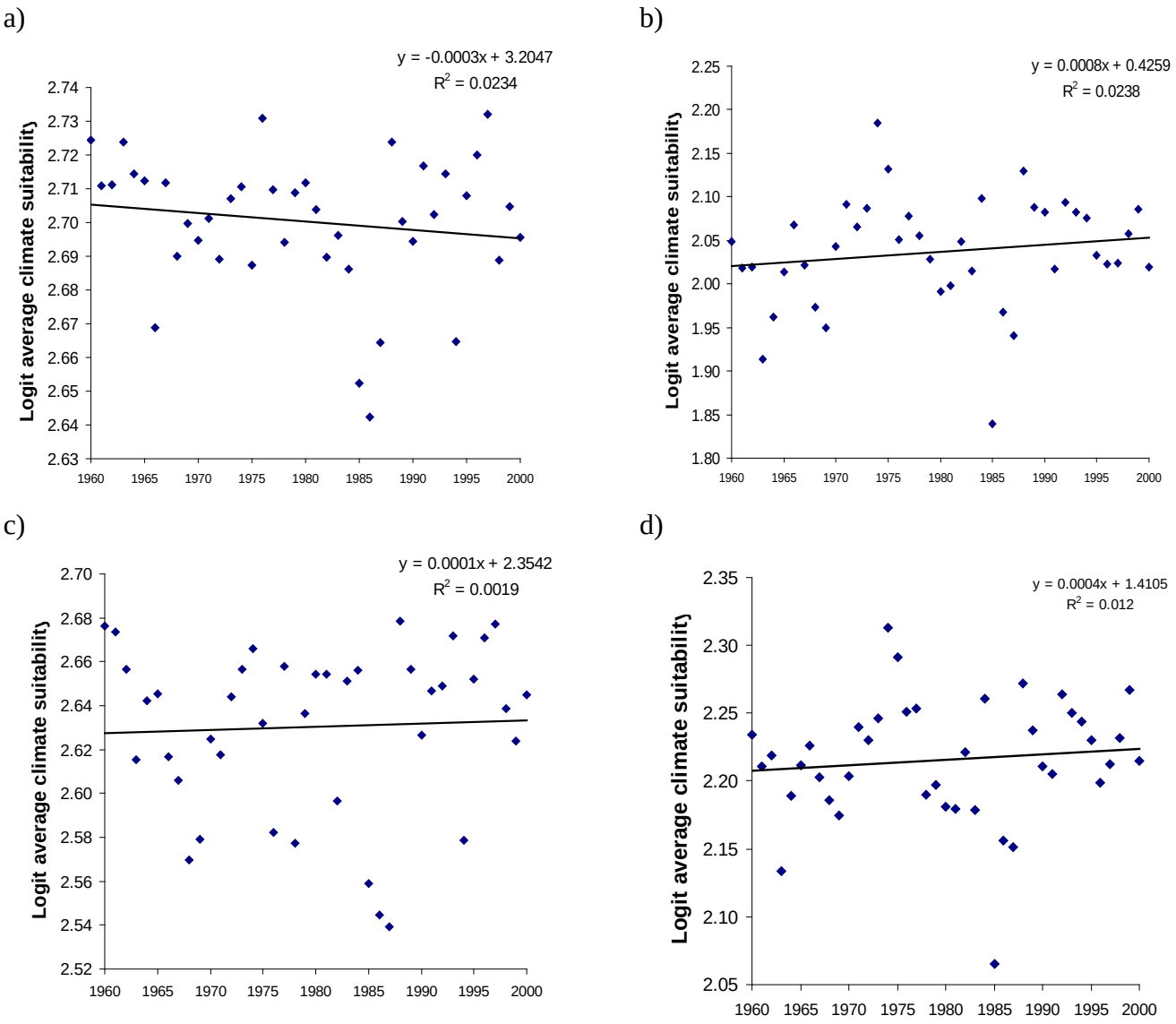


Figure 5.10: Logit average climate suitability and trend for *Sylvia atricapilla* for a) GAM breeding model, b) GAM non-breeding model, c) CRS breeding model and d) CRS non-breeding model

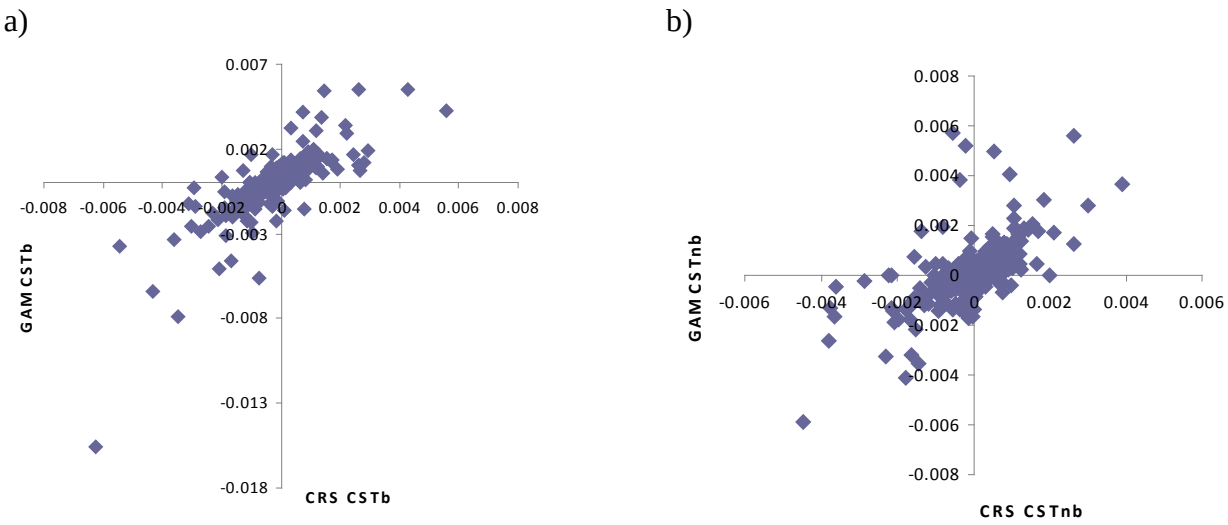
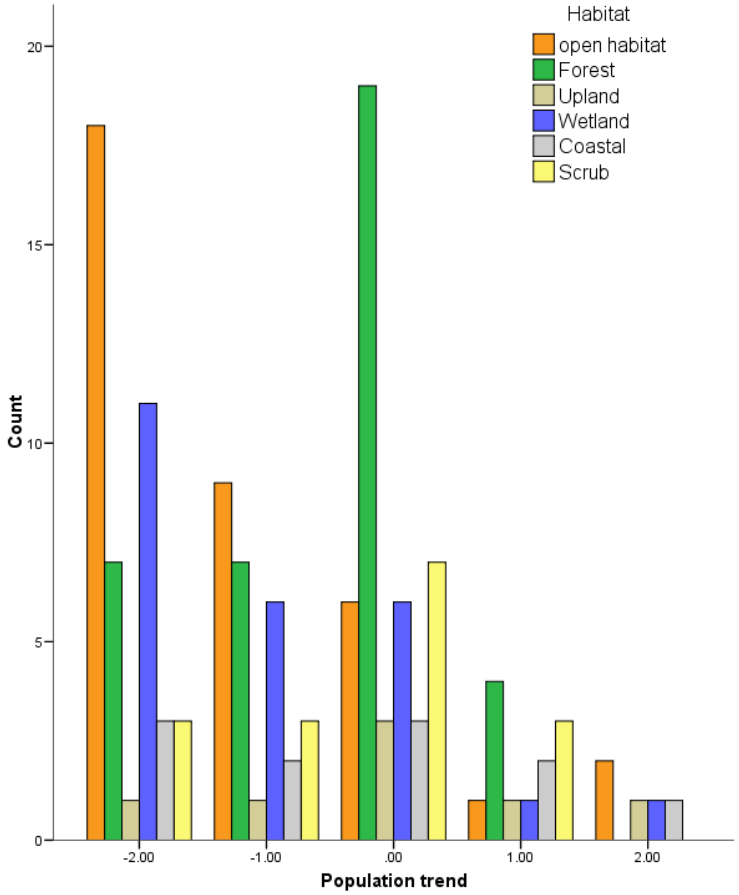


Figure 5.11: Relationship between GAM and CRS a) breeding climate suitability trend and b) non-breeding climate suitability trend across species

Population change

Figure 5.12 shows that the majority of species' populations were either stable or declining in Europe during the two time periods. A Kruskal-Wallis test showed that species' habitat affected species' categorisation for the 1970-1990 period (H_6= 15.36, $p < 0.05$) but not for the 1990-2000 period (H_6= 6.24, $p = 0.397$). A greater proportion of species residing in open habitat and wetland habitat declined during the first time period, whilst the majority of forest species' populations remained stable (Fig.5.12). Grouping (passerine or non-passerine) affected species' categorisation for both time periods (1970-1990 period: H_1= 5.29, $p < 0.05$; 1990-2000 period: H_1= 4.99, $p < 0.05$) with a greater proportion of non-passerines declining. Migratory category affected species' categorisation for the 1990-2000 period (H_2= 6.09, $p < 0.05$) but the effect was not statistically significant for the 1970-1990 period (H_2= 5.38, $p = 0.068$). Short-distance migrant population trends tended to stay stable (50% stable, 30% declining and 20% increasing), trans-Saharan migrants declined (60% declining) and split-strategy migrants varied in their response (49% declining, 31% stable; 20% increasing; Fig. 5.13). Neither breeding biome nor non-breeding biome affected species' population trend (1970-1990 period: breeding biome: H_6 = 9.82, $p = 0.133$, non-breeding: H_5 = 10.64, $p = 0.059$; 1990-2000 period: breeding biome: H_6 = 1.40, $p = 0.965$, non-breeding: H_5 = 5.23, $p = 0.389$).

a)



b)

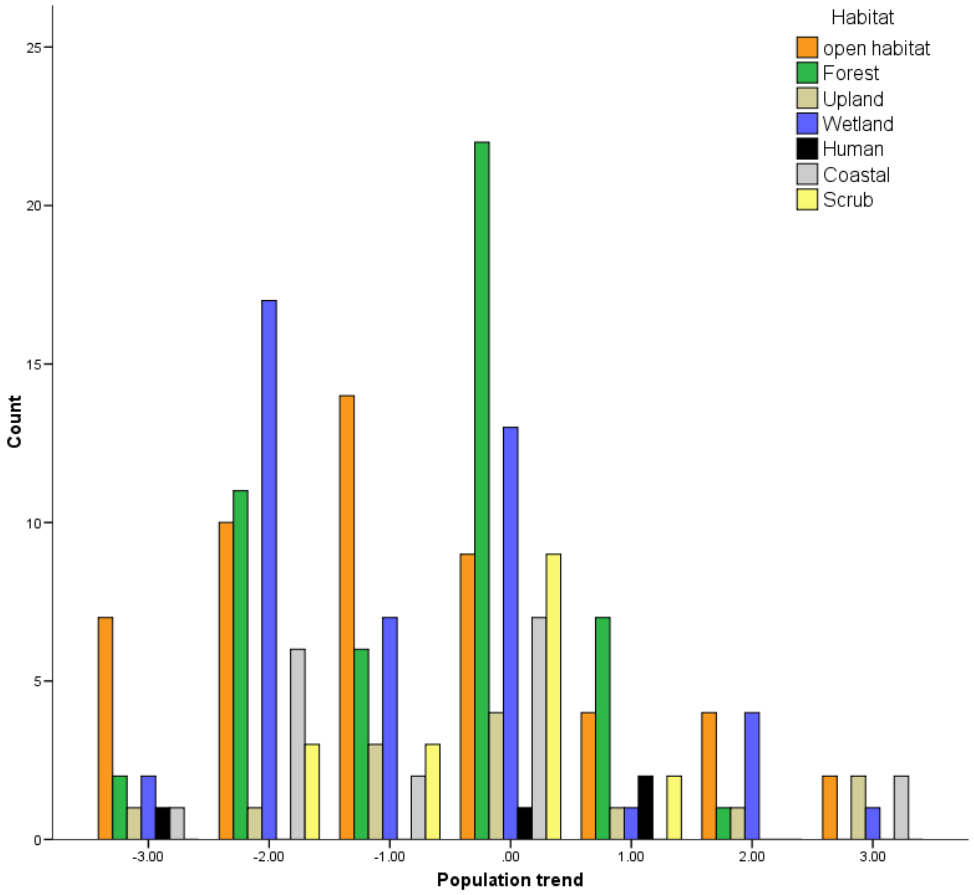


Figure 5.12: Frequency of species in each population trend category by habitat category for a) 1970 to 1990 where -2= large decline, -1= small decline, 0= stable, 1= small increase and 2= large increase; b) 1990-2000 where -3= large decline, -2= moderate decline, -1= small decline, 0= stable, 1= small increase, 2= moderate increase and 3= large increase.

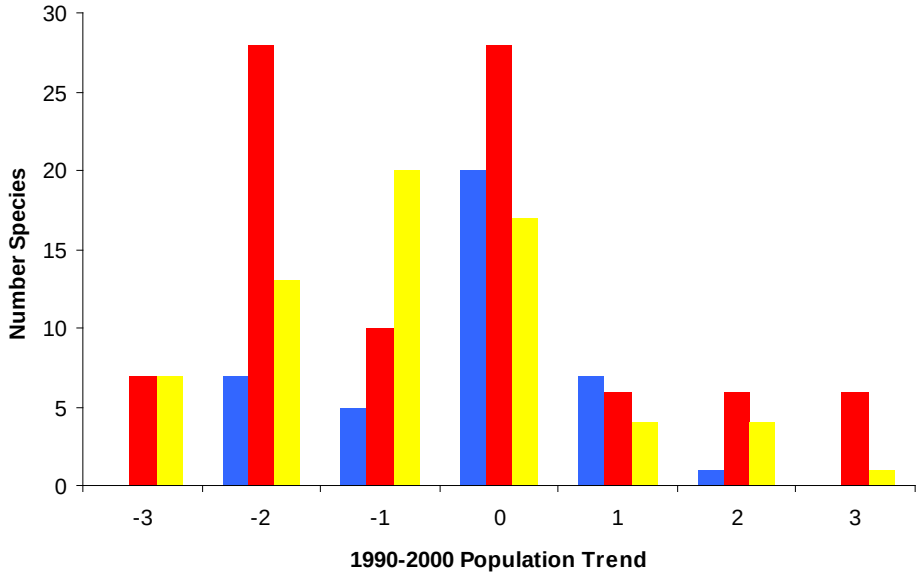


Figure 5.13: Number of species in each migratory category for the 1990-2000 trend where -3= large decline, -2= moderate decline, -1= small decline, 0= stable, 1= small increase, 2= moderate increase and 3= large increase. Blue = European migrants, red = split-strategy migrants and yellow = Trans-Saharan migrants.

Separate Kruskall-Wallis tests revealed that none of the tested variables was significant for late breeding non-passerines in either time period. Early breeding non-passerines, those that breed within the first two year, were affected by migratory strategy (H_2= 6.41, $p < 0.05$) and non-breeding biome (H_4= 10.45, $p < 0.05$) for the 1970-1990 period. For passerines, habitat had an effect on population trends for the 1970-1990 period (H_4= 11.80, $p < 0.05$).

Models of population change

All species

Models that were retained for the 1970-1990 data included either both breeding and non-breeding climate trends together or non-breeding climate trends alone, along with the base models (Table 5.8). Analyses of deviance (log-likelihood tests) revealed that GAM and CRS climatic models were not significantly different from each other. The base model was significantly better than the null model ($LR_6 = 21.64$, $p < 0.01$) and all models were significantly better than the null model.

AIC model selection showed that the best model was the base model plus GAM CSTnb with a two-year time lag, closely followed by the equivalent CRS model (Table 5.8). Residual deviance analysis also confirmed that the inclusion of these climatic variables improved the base model (Table 5.8).

Table 5.8: Ordinal regression Statistics for all species with 1970-1990 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model and BaseΔdev is the difference in deviance with the base model. * denotes 0.05 significance level; ** denotes significance at 0.001 level.

Model	Residual Deviance	no. Estim.	d.f.	Over-dispersion	NullΔdev	Base Δdev	AIC	ΔAIC
Base + GAM CSTnb $_{t=-2}$	342.95	11	121	2.83	27.30**	5.66*	364.95	0.00
Base + CRS CSTnb $_{t=-2}$	344.11	11	121	2.84	26.14**	4.50*	366.11	1.16
Base + GAM climate $_{t=-2}$	342.65	12	120	2.86	27.60**	5.96*	366.65	1.70
Base + GAM CSTb$_{t=-1}$+ CSTnb$_{t=-2}$	342.91	12	120	2.86	27.34**	5.70*	366.91	1.96
Base + CRS CSTb $_{t=-1}$+ CSTnb $_{t=-2}$	342.94	12	120	2.86	27.31**	5.67	366.95	2.00
Base +CRS climate $_{t=-2}$	343.06	12	120	2.86	27.19**	5.55*	367.06	2.11
Base + CRS CSTnb $_{t=-1}$	345.33	11	121	2.85	24.92**	3.28	367.39	2.44
Base + GAM CSTnb $_{t=-1}$	346.11	11	121	2.86	24.14**	2.50	368.11	3.16
Base + GAM CSTb$_{t=0}$ + CSTnb$_{t=-1}$	344.16	12	120	2.87	26.09**	4.45	368.16	3.21
Base + CRS climate $_{t=-1}$	344.20	12	120	2.87	26.05**	4.41	368.20	3.25
Base (Habitat + Order)	348.61	10	122	2.86	21.64**		368.61	3.66
Base + CRS CSTb $_{t=0}$ + CSTnb $_{t=-1}$	344.99	12	120	2.87	25.26**	3.62	368.99	4.04
Base + CRS CSTnb$_{t=0}$	348.09	11	121	2.88	22.16**	0.52	370.09	5.14
Base + GAM CSTnb $_{t=0}$	348.09	11	121	2.88	22.16**	0.52	370.09	5.14
Base + GAM climate $_{t=-1}$	346.10	12	120	2.88	24.15**	2.51	370.09	5.14
Base+ GAM climate $_{t=0}$	346.55	12	120	2.89	23.70**	2.06	370.58	5.63
Base + CRS climate$_{t=0}$	347.93	12	120	2.90	22.32**	0.68	371.93	6.98
Null	370.25	4	128	2.89			378.25	13.30

For the best full model, the coefficients and associated standard error and Wald statistic are shown in Table 5.9. CSTnb showed an effect on population trend. However, the standard error was large. In fact, the over-dispersion in the model (Table 5.8) was very high, which suggests that the predictor variables do not explain the population trends very well. Correcting the values for over-dispersion (Johnson and Albert, 1999) in the models revealed that none of the models was significantly different from the base model (though they were better than the null model).

Table 5.9: Estimated coefficients for the ordinal regression (population trend ~ GAM climate (t = -2) + habitat + order)

Variables	Value	Std. Error	t value	Wald	p
GAM $CSTb_{t=-2}$	14.57	28.25	0.52	0.27	> 0.05
GAM $CSTnb_{t=-2}$	-94.25	39.62	-2.38	5.65	< 0.05
Forest species	0.84	0.31	2.71	7.32	< 0.01
Upland species	1.02	0.49	2.05	4.18	< 0.05
Wetland species	0.44	0.37	1.19	1.42	> 0.05
Coastal species	1.09	0.45	2.41	5.79	< 0.05
Scrub species	0.56	0.39	1.43	2.05	> 0.05
Order	0.72	0.26	2.74	7.53	< 0.01

Table 5.10 shows the distribution of predicted values (highest probability) from the null model and the best model. Both of these were significantly different from the observed trend (Null: χ^2_3=255.2, p< 0.0001; Best model: χ^2_3= 66.02, p<0.001). The null model predicted correct trends for 45 species and wrong trends for 87 species. The best model predicted 61 correct trends and 71 wrongly predicted trends. Chi-square showed that the best model was significantly better than the null model (χ^2_1= 8.63, p<0.01). Examining only trends (decrease/stable/increase), the null model correctly predicted 71 (53%) trends and the best model 82 (62%). In this case the best model was marginally better than the null model (χ^2_1= 3.69, p=0.05). Out of those wrongly predicted, eleven species were predicted to have opposite trends: *Gyps fulvus*, *Falco eleonorae*, *Falco peregrinus*, *Grus grus*, *Pandion haliaetus*, *Ciconia nigra*, *Netta rufina*, *Larus fuscus*, *Chlidonias hybridus*, *Hippolais pallid* and *Sylvia melanothorax* all show overall small increases during that time, but were predicted to decrease.

Table 5.10: Frequency of population category for the 1970-1990 period, in truth and as predicted by the null model and the best model (see Table 5.8)

Population trend	Observed	Null	Best model
Large decrease	43	0	65
Small decrease	28	0	0
Stable	45	132	67
Small increase	16	0	0
Large increase	0	0	0

Models that were retained for the 1990-2000 data included either both breeding and non-breeding climate trends or non-breeding climate trends along with the base models (Table 5.11). Models using GAM or CRS climates with time lags were different according to the log-likelihood tests (LR stat $_{\text{climate } t = -1} = 3.25$, $p < 0.001$; LR stat $_{\text{CSTb } t = -1} = 3.26$, $p < 0.001$; LR stat $_{\text{climate } t = -2} = 2.57$, $p < 0.001$; LR stat $_{\text{CSTb } t = -2} = 2.60$, $p < 0.001$; LR stat $_{\text{CSTb } t = -1 + \text{CSTnb } t = -2} = 3.26$, $p < 0.001$). The base model was significantly different from the null model ($LR_3=17.45$, $p < 0.001$) and consequently all models were significantly better than the null model (NullΔdev in Table 5.11).

AIC model selection showed that the best model was the base model plus CRS CSTb with a two-year time lag, closely followed by base model plus CRS CSTb with one-year time lag (Table 5.11). Residual deviance analyses also confirmed that the inclusion of these climatic variables improved the base model (BaseΔdev in Table 5.11).

Table 5.11: Ordinal regression Statistics for all species with 1990-2000 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model and BaseΔdev is the difference in deviance with the base model. * denotes 0.05 significance level; ** denotes significance at 0.001 level.

Model	Deviance	no. Estim	d.f.	Over dispersion	NullΔdev	Base Δdev	AIC	ΔAIC
Base + CRS CSTb $_{t = -2}$	640.34	10	186	3.44	21.98**	4.52*	660.35	0.00
Base + CRS CSTb $_{t = -1}$	640.40	10	186	3.44	21.92**	4.46*	660.40	0.05
Base + CRS climate $_{t = -2}$	640.25	11	185	3.46	22.07**	4.61*	662.25	1.90
Base + CRS CSTb$_{t=-1}$+ CSTnb$_{t=-2}$	640.29	11	185	3.46	22.03**	4.57*	662.29	1.94
Base +CRS climate $_{t = -1}$	640.35	11	185	3.46	21.97**	4.51*	662.35	2.00
Base + GAM CSTb $_{t = 0}$	642.83	10	186	3.46	19.49**	2.03	662.83	2.48
Base (Migratory strategy + order)	644.86	9	187	3.45	17.46**		662.86	2.51
Base + GAM CSTb $_{t = -2}$	642.95	10	186	3.46	19.37**	1.91	662.95	2.60
Base + GAM CSTb $_{t = -1}$	643.66	10	186	3.46	18.66**	1.20	663.66	3.31
Base + CRS CSTb $_{t = 0}$	644.35	10	186	3.46	17.97**	0.51	664.35	4.00
Base + GAM climate $_{t = 0}$	642.63	11	185	3.47	19.69**	2.23	664.63	4.28
Base + GAM climate $_{t = -2}$	642.83	11	185	3.47	19.49**	2.03	664.83	4.48
Base + GAM CSTb$_{t=-1}$+ CSTnb$_{t=-2}$	643.52	11	185	3.48	18.80**	1.34	665.52	5.17
Base + GAM climate $_{t = -1}$	643.59	11	185	3.48	18.73**	1.27	665.59	5.24
Base + CRS climate $_{t = 0}$	644.34	11	185	3.48	17.98**	0.52	666.34	5.99
Null	662.32	6	190	3.49			674.32	13.97

For the best full model, the coefficients and associated standard error and Wald statistic are shown in Table 5.12. Breeding CST showed an effect on population trend. The over-dispersion in the model (Table 5.11) was very high which suggests that the predictor variables are not explaining the population trends very well. Correcting the values for over-dispersion

(Johnson and Albert, 1999) in the models revealed that none of the models was significantly different from the base model (though they were better than the null model).

Table 5.12: Estimated coefficients for the ordinal regression (population trend ~ CRS climate (t = -2) + migratory category + order)

	Value	Std. Error	t value	Wald	p
CRS $CSTb_{t=-2}$	-1.71	0.57	-3.00	9.01	<0.01
CRS $CSTnb_{t=-2}$	3.90	13.56	0.29	0.08	>0.05
Split strategy migrants	-0.39	0.23	-1.69	2.88	>0.05
Trans-Saharan migrants	-0.61	0.25	-2.44	5.96	<0.05
Order	0.50	0.17	2.91	8.47	<0.01

Table 5.13 shows the distribution of predicted values (highest probability) from the null model and the best model. Both of these were significantly different from the true trends (Null: χ^2_6=395.01, p< 0.0001; Best model: χ^2_6= 148.98, p<0.001). The null model predicted correct trends for 65 species and wrong trends for 131 species. The best model predicted 71 correct trends and 125 wrongly assigned trends. Chi-square showed that the best model was not significantly better than the null model (χ^2_1= 0.828, p= 0.362). Examining only trends (decrease/stable/increase), the null model correctly predicted 97 (49%) trends and the best model 106 (54%). In this case, the best model was not significantly better than the null model (χ^2_1= 3.14, p=0.07).

Twenty-one species were predicted to have opposite trends to those observed for the species: *Gyps fulvus*, *Accipiter nisus*, *Buteo buteo*, *Falco peregrinus*, *Circus aeruginosus*, *Circus pygargus*, *Egretta alba*, *Egretta garzetta*, *Anthropoides virgo*, *Grus grus*, *Larus fuscus*, *Pandion haliaetus*, *Ardea cinerea*, *Netta rufina*, *Sterna caspia*, *Bubulcus ibis*, *Carpospiza brachydactyla*, *Merops apiaster*, *Tachymarptis melba*, *Hippolais languida* and *Saxicola torquatus* all have increasing population trends but were predicted to decrease.

Table 5.13: Frequency of population category for the 1990-2000 period, in truth and as predicted by the null model and the best model (see Table 5.11).

Population trend	Observed	Null	Best model
Large decrease	14	0	0
Moderate decrease	48	0	98
Small decrease	35	0	0
Stable	65	196	97
Small increase	17	0	0
Moderate increase	10	0	0
Large increase	7	0	1

Non-passerines

Models that were retained for the 1970-1990 data for all non-passerine species included either both breeding and non-breeding climate trends or non-breeding climate trends (Table 5.14). Analyses of deviance revealed that GAM and CRS climatic models were not significantly different.

AIC model selection showed that the best model was GAM climate with a four-year time lag, followed by GAM CSTb with a four-year time lag. Analyses of residual deviance confirmed that these models were different from the null model (Table 5.14).

The Wald statistic indicated that GAM CSTb with a four-year time lag had an effect on non-passerines population (Wald = 4.27, $p < 0.05$) as did GAM CSTnb with a four-year time lag (Wald = 4.49, $p < 0.05$). However, all models were not significantly better than the null model when over-dispersion is taken into account. Furthermore, the standard errors for the two above variables are large (55.63 and 82.48 respectively).

Table 5.14: Ordinal regression statistics for non-passerines with 1970-1990 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model. .* denotes 0.05 significance level.

Model	Deviance	no. Estim	d.f.	Over-dispersion	NullΔdev	AIC	ΔAIC
GAM climate$_{t = -4}$	178.95	6	70	2.56	8.71*	188.95	0.00
GAM CSTb$_{t= -4}$	181.78	5	71	2.56	5.88*	189.79	0.84
GAM climate$_{t = -3}$	180.52	6	70	2.58	7.14*	190.52	1.57
GAM CSTnb$_{t= -4}$	183.43	5	71	2.58	4.23	191.43	2.48
GAM CSTb$_{t= -5}$	183.15	5	71	2.58	4.51	191.85	2.90
GAM climate$_{t = -5}$	181.88	6	70	2.60	5.78	191.88	2.93
GAM CSTnb$_{t= -3}$	184.05	5	71	2.59	3.61	192.05	3.10
GAM CSTb$_{t= -3}$	184.51	5	71	2.60	3.15	192.51	3.56
GAM CSTnb$_{t= -2}$	184.74	5	71	2.60	2.92	192.75	3.80
GAM CSTnb$_{t= -5}$	184.81	5	71	2.60	2.85	192.81	3.86
GAM CSTb$_{t=0}$	185.40	5	71	2.61	2.26	193.40	4.45
CRS CSTnb$_{t= -1}$	185.59	5	71	2.61	2.07	193.59	4.64
Null	187.66	4	72	2.61		193.66	4.71
CRS CSTnb$_{t= -2}$	185.66	5	71	2.61	2.00	193.66	4.71
CRS climate$_{t = -1}$	183.85	6	70	2.63	3.81	193.85	4.90
GAM CSTnb$_{t= -1}$	186.06	5	71	2.62	1.60	194.06	5.11
CRS CSTb$_{t= -1}$	186.26	5	71	2.62	1.40	194.26	5.31
CRS climate$_{t = -2}$	184.31	6	70	2.63	3.35	194.31	5.36
GAM climate$_{t = -2}$	184.40	6	70	2.63	3.26	194.40	5.45
CRS CSTb$_{t= -2}$	186.43	5	71	2.63	1.23	194.43	5.48
CRS CSTb$_{t= -5}$	186.58	5	71	2.63	1.08	194.58	5.63
CRS CSTb$_{t= -4}$	186.59	5	71	2.63	1.07	194.59	5.64
CRS CSTnb$_{t= -4}$	186.69	5	71	2.63	0.97	194.69	5.74
CRS CSTnb$_{t= -3}$	186.72	5	71	2.63	0.94	194.72	5.77
CRS CSTb$_{t= -3}$	186.84	5	71	2.63	0.82	194.84	5.89
GAM CSTb$_{t= -2}$	186.91	5	71	2.63	0.75	194.91	5.96
CRS CSTnb$_{t= -5}$	186.99	5	71	2.63	0.67	194.99	6.04
GAM climate$_{t = 0}$	185.32	6	70	2.65	2.34	195.32	6.37
GAM CSTb$_{t= -1}$	187.35	5	71	2.64	0.31	195.35	6.40
CRS climate$_{t = -5}$	185.94	6	70	2.66	1.72	195.44	6.49
CRS CSTb$_{t=0}$	187.47	5	71	2.64	0.19	195.47	6.52
CRS CSTnb$_{t=0}$	187.49	5	71	2.64	0.17	195.49	6.54
GAM CSTnb$_{t=0}$	187.58	5	71	2.64	0.08	195.58	6.63
CRS climate$_{t = -3}$	185.86	6	70	2.66	1.80	195.66	6.71
CRS climate$_{t = -4}$	185.68	6	70	2.65	1.98	195.68	6.73
GAM climate$_{t = -1}$	186.06	6	70	2.66	1.60	196.06	7.11
CRS climate$_{t = 0}$	187.27	6	70	2.68	0.39	197.27	8.32

Despite considerable variation there was a significant positive correlation between GAM CSTb with a four-year time lag and population trend (Fig. 514a; Spearman rho = 0.26, $p<0.05$). However, there was no significant correlation between GAM CSTnb with a four-year time lag and population trend (Fig. 514b; Spearman rho = -0.11, $p = 0.30$).

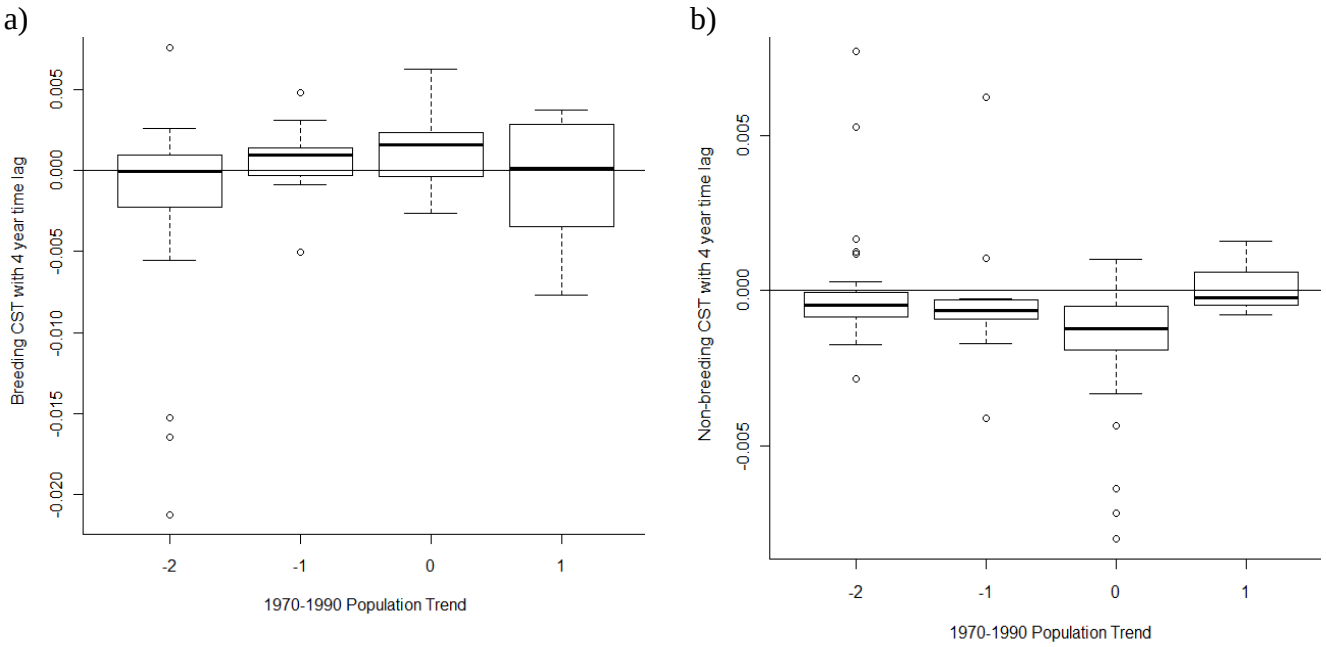


Figure 5.14: Non-passerine population trend during the 1970-1990 period and Climate Suitability Trend (CST) as modeled by GAM with a 4-year time lag; a) breeding CST and b) non-breeding CST.

Table 5.15 shows the models retained for non-passerine species that breed in the first two years for the 1970-1990 period. Analyses of deviance revealed that GAM and CRS climatic models were not significantly different. However, AIC selection indicated that CRS climate models were not useful (ΔAIC>7). All retained models were significantly different from the null model. ΔAIC values show that the best model was non-breeding biome plus GAM climate with a five-year time lag. This model was significantly different from the null and the base model when over-dispersion is taken into account.

Table 5.15: Ordinal regression statistics for 1-2 year breeding non-passerines with 1970-1990 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model. .** denotes 0.001 significance level, .

Model	Deviance	no. Estim	d.f.	Over-dispersion	NullΔdev	AIC	ΔAIC
Base + GAM climate$_{t = -5}$	81.44	12	34	2.46	27.57**	99.43	0.00
Base + GAM climate$_{t = -3}$	83.88	12	33	2.54	25.13**	101.88	2.44
Base + GAM climate$_{t = -4}$	83.90	12	34	2.54	25.11**	101.90	2.46
Base + GAM CSTnb$_{t= -4}$	86.52	11	33	2.54	22.49**	102.51	3.07
Base + GAM CSTnb$_{t= -3}$	86.77	11	33	2.55	22.23**	102.77	3.33
Base + GAM CSTnb$_{t= -5}$	87.48	11	33	2.57	21.52**	103.48	4.04
Base + GAM CSTnb$_{t= -2}$	89.20	11	34	2.62	19.81**	105.20	5.76
Base + GAM CSTb$_{t= -3}$	91.45	11	34	2.62	17.56**	107.45	7.56
Base + GAM CSTb$_{t= -5}$	92.09	11	33	2.71	16.92**	108.09	8.65
Base (Non-breeding biome)	94.38	7	39	2.42	17.24**	108.38	8.94
Base + GAM CSTb$_{t= -4}$	92.54	11	33	2.72	16.47**	108.54	9.11
Null	109.01	3	42	2.60		115.01	15.57

Table A27 details each species' individual climatic suitability trend for the best model time frame showing how weak individual species' trends are (see above) with only four species having significant trends. *Nycticorax nycticorax* had a near significant negative CSTnb. *Falco subbuteo* had a near significant negative CSTb, *Falco peregrinus* had a negative CSTb whilst its population is increasing, and *Vanellus vanellus* had a significant positive CSTb.

Table 5.16 shows the models retained for late breeding non-passerine species (those that breed after the first two years) for the 1970-1990 period. Analyses of deviance reveal that GAM and CRS climatic models were not significantly different. ΔAIC values showed that the best model was GAM CSTb with a four-year time lag, followed by GAM CSTb with a three-year time lag (Table 5.16). However, all models were not significantly better than the null model when over-dispersion is taken into account.

Table 5.16: Ordinal regression statistics for above 2 year breeding non-passerines with 1970-1990 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model. * denotes 0.05 significance level.

Model	Deviance	no. Estim	d.f.	Over-dispersion	NullΔdev	AIC	ΔAIC
GAM $CSTb_{t=-4}$	69.54	4	26	2.67	5.30*	77.55	0.00
GAM $CSTb_{t=-3}$	70.65	4	26	2.72	4.19*	78.65	1.11
GAM $CSTb_{t=-5}$	70.72	4	26	2.72	4.12*	78.72	1.17
GAM $climate_{t=-5}$	68.90	5	25	2.76	5.94*	78.90	1.35
GAM $climate_{t=-4}$	69.50	5	25	2.78	5.34	79.50	1.95
GAM $climate_{t=-3}$	69.73	5	25	2.79	5.11	79.72	2.17
Null	74.84	3	27	2.77		80.84	3.29
CRS $CSTnb_{t=-4}$	74.07	4	26	2.85	0.77	82.07	4.52
CRS $CSTb_{t=-4}$	74.09	4	26	2.85	0.75	82.09	4.54
CRS $CSTb_{t=-5}$	74.09	4	26	2.85	0.75	82.09	4.54
CRS $CSTb_{t=-3}$	74.13	4	26	2.85	0.71	82.13	4.58
GAM $CSTnb_{t=-3}$	74.64	4	26	2.87	0.20	82.64	5.09
CRS $CSTnb_{t=-5}$	74.68	4	26	2.87	0.16	82.68	5.14
GAM $CSTnb_{t=-5}$	74.85	4	26	2.88	-0.01	82.85	5.30
GAM $CSTnb_{t=-4}$	75.03	4	26	2.89	-0.19	83.03	5.48
CRS $CSTnb_{t=-3}$	75.05	4	26	2.89	-0.21	83.06	5.51
CRS $climate_{t=-4}$	73.40	5	25	2.94	1.44	83.40	5.85
CRS $climate_{t=-5}$	73.84	5	25	2.95	1.00	83.84	6.29
CRS $climate_{t=-3}$	74.37	5	25	2.98	0.46	84.38	6.83

Table A28 details each species' individual climatic suitability trend for the best model time frame. For CSTb, only *Larus genei* had a significant CST which is positive. For CSTnb only *Burhinus oedicnemus* had a significant CST which is positive while the population is currently declining.

Models that were retained for all non-passerines for the 1990-2000 data included either breeding and non-breeding climate trends together or non-breeding climate trends alone (Table 5.17). Analyses of deviance revealed that GAM and CRS climatic models were not significantly different from each other.

AIC model selection showed that the best model was GAM CSTb with a five-year time lag, followed GAM CSTb with a two-year time lag (Table 5.17). Analyses of residual deviance confirmed that these models were different from the null model.

The Wald statistic indicated that GAM CSTb with a five-year time lag had an effect on non-passerine populations (Wald = 4.84, $p < 0.05$) though GAM CSTnb with a five-year time lag did not (Wald = 0.62, $p > 0.05$). However, all models were not significantly better than the null model when correcting for over-dispersion.

Table 5.17: Ordinal regression statistics for non-passerines with 1990-2000 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model. * denotes significance at the 0.05 level.

Model	Deviance	no. Estim	d.f.	Over-dispersion	nullΔdev	AIC	ΔAIC
GAM $CSTb_{t= -5}$	391.30	7	106	3.69	5.13*	405.30	0.00
GAM $CSTb_{t= -2}$	391.45	7	106	3.69	4.98*	405.45	0.15
CRS $CSTb_{t= -2}$	390.10	7	106	3.68	6.33*	406.10	0.80
GAM $CSTb_{t=0}$	393.15	7	106	3.71	3.28	407.15	1.85
CRS $CSTb_{t= -1}$	393.17	7	106	3.71	3.26	407.17	1.87
GAM $climate_{t = -5}$	391.24	8	105	3.73	5.19*	407.24	1.94
GAM $climate_{t = -2}$	391.35	8	105	3.73	5.08	407.35	2.05
CRS $climate_{t = -3}$	393.47	8	105	3.75	2.96	407.47	2.17
GAM $CSTb_{t= -1}$	394.00	7	106	3.72	2.43	408.00	2.70
GAM $CSTb_{t= -4}$	394.12	7	106	3.72	2.31	408.12	2.82
GAM $climate_{t = -3}$	392.22	8	105	3.74	4.21	408.22	2.92
Null	396.43	6	107	3.70		408.43	3.13
CRS $CSTb_{t=0}$	394.54	7	106	3.72	1.89	408.54	3.24
GAM $climate_{t = 0}$	392.71	8	105	3.74	3.72	408.71	3.41
CRS $climate_{t = -2}$	392.92	8	105	3.74	3.51	408.92	3.62
CRS $climate_{t = -1}$	393.00	8	105	3.74	3.43	409.00	3.70
GAM $climate_{t = -1}$	393.40	8	105	3.75	3.03	409.40	4.10
GAM $climate_{t = -4}$	393.70	8	105	3.75	2.73	409.70	4.40
GAM $CSTb_{t= -3}$	396.00	7	106	3.74	0.43	410.00	4.70
CRS $climate_{t = 0}$	394.02	8	105	3.75	2.41	410.02	4.72

There was considerable variation in 5 year lagged CST within each population trend category and the trends were centred around zero, showing no significant correlation (Fig 5.15; breeding: Spearman rho = 0.085, p=0.370; non-breeding Spearman rho = 0.046, p=0.624).

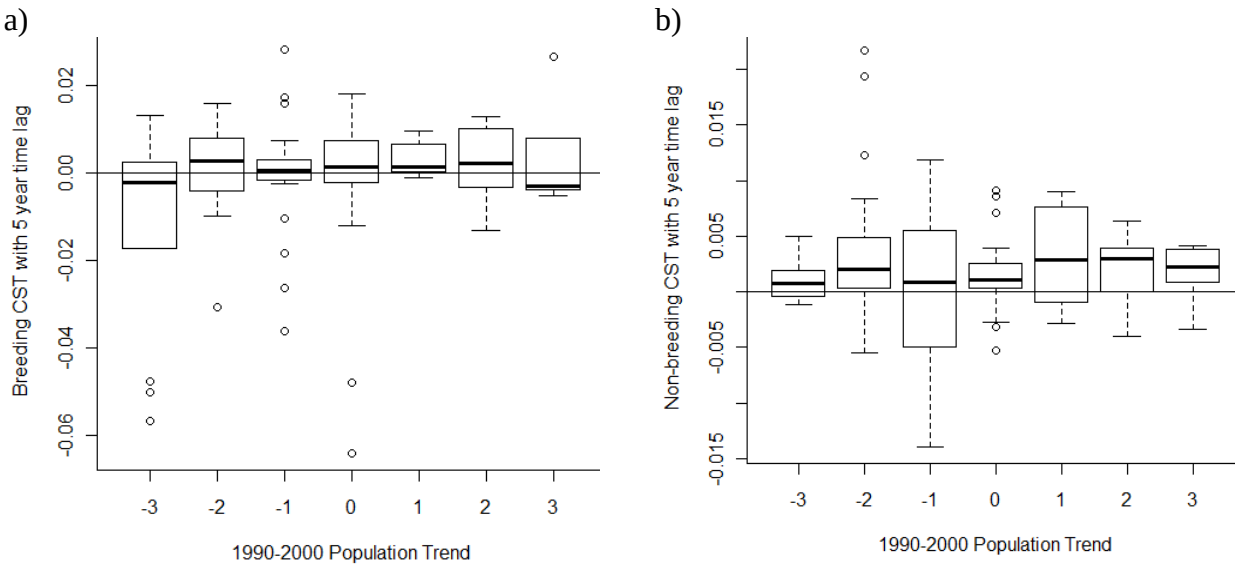


Figure 5.15: Non-passerine population trend during the 1990-2000 period and Climate Suitability Trend (CST) as modelled by GAM with a 5-year time lag: a) breeding CST and b) non-breeding CST.

Table 5.18 shows the models retained for early breeding non-passerine species for the 1990-2000 time period. Analyses of deviance revealed that GAM and CRS climatic models were not significantly different. ΔAIC values showed that the best model was GAM CSTnb with a three-year time lag (Table 5.18). However, all models were not significantly better than the null model when over-dispersion, which was high, is taken into account.

Table A27 details each species' individual climatic suitability trend for the best model time frame. No species had a significant CST. This is unsurprising given the climate models' deviances were very close to the null model.

Table 5.18: Ordinal regression statistics for early breeding non-passerines with 1990-2000 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model. * denotes significance at the 0.05 level.

Model	Deviance	no. Estim	d.f.	Over-dispersion	NullΔdev	AIC	ΔAIC
GAM $CSTnb_{t= -3}$	215.74	6	65	3.36	2.57	230.29	0.00
Null	218.30	5	66	3.31		228.31	0.57
GAM $climate_{t = -3}$	214.98	7	64	3.36	3.32	230.30	1.25
CRS $CSTnb_{t=0}$	217.40	6	65	3.34	0.27	229.42	1.67
CRS $CSTnb_{t= -1}$	217.40	6	65	3.34	0.27	229.48	1.74
CRS $CSTnb_{t= -2}$	217.82	6	65	3.35	0.15	229.82	2.08
GAM $CSTb_{t= -1}$	217.99	6	65	3.35	0.32	231.99	2.25
CRS $CSTnb_{t= -3}$	218.09	6	65	3.36	0.07	230.00	2.26
CRS $CSTb_{t= -1}$	218.03	6	65	3.35	0.08	230.03	2.29
GAM $CSTnb_{t= -4}$	218.00	6	65	3.36	0.31	230.19	2.32
CRS $CSTb_{t= -2}$	218.07	6	65	3.36	0.07	230.07	2.33
GAM $CSTb_{t=0}$	218.08	6	65	3.36	0.23	231.93	2.34
CRS $CSTb_{t= -3}$	218.08	6	65	3.36	0.07	230.09	2.35
CRS $CSTnb_{t= -5}$	218.15	6	65	3.36	0.05	230.16	2.42
GAM $CSTb_{t= -4}$	218.10	6	65	3.35	0.21	231.99	2.45
CRS $CSTnb_{t= -4}$	218.20	6	65	3.36	0.03	230.20	2.46
GAM $CSTnb_{t=0}$	218.23	6	65	3.36	0.08	230.08	2.50
CRS $CSTb_{t=0}$	218.25	6	65	3.36	0.01	230.25	2.51
GAM $CSTb_{t= -2}$	218.24	6	65	3.36	0.06	232.20	2.51
GAM $CSTnb_{t= -1}$	218.28	6	65	3.36	0.03	229.99	2.54
CRS $CSTb_{t= -5}$	218.29	6	65	3.36	0.01	230.29	2.55
GAM $CSTb_{t= -3}$	218.29	6	65	3.52	0.02	228.99	2.55
CRS $CSTb_{t= -4}$	218.30	6	65	3.36	0.00	230.30	2.56
GAM $CSTnb_{t= -2}$	218.30	6	65	3.36	0.00	230.25	2.56
GAM $CSTb_{t= -5}$	218.30	6	65	3.36	0.01	232.30	2.57
GAM $CSTnb_{t= -5}$	218.30	6	65	3.36	0.01	230.31	2.57
CRS $climate_{t = -1}$	216.84	7	64	3.39	0.43	230.84	3.10
CRS $climate_{t = -2}$	217.28	7	64	3.40	0.30	231.28	3.54
CRS $climate_{t = 0}$	217.30	7	64	3.40	0.30	231.40	3.66
CRS $climate_{t = -3}$	217.85	7	64	3.40	0.13	231.86	4.12
GAM $climate_{t = 0}$	217.92	7	64	3.41	0.38	228.31	4.19
GAM $climate_{t = -1}$	217.99	7	64	3.41	0.32	230.24	4.25
GAM $climate_{t = -4}$	217.99	7	64	3.37	0.32	227.74	4.25
CRS $climate_{t = -5}$	218.11	7	64	3.41	0.06	232.10	4.36
CRS $climate_{t = -4}$	218.10	7	64	3.41	0.06	232.19	4.45
GAM $climate_{t = -2}$	218.23	7	64	3.41	0.07	230.28	4.46
GAM $climate_{t = -5}$	218.30	7	64	3.41	0.01	230.06	4.56

Table 5.19 shows the models retained for late breeding non-passerine species for the 1990-2000 period. Analyses of deviance revealed that GAM and CRS climatic models were not significantly different. ΔAIC values showed that the best model was CRS CSTb with a two-year time lag, followed by GAM CSTb with a five-year time lag (Table 5.19). However, all models were not significantly better than the null model when over-dispersion is taken into account. Indeed the over-dispersion was very high indicating poor model fit. Table A28 shows that only two species have significant CSTnb: *Circus aeruginosus* and *Egretta alba* with significant positive trends concurring with the population increases during that time period.

Table 5.19: Ordinal regression statistics for late breeding non-passerines with 1990-2000 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model. * denotes significance at the 0.05 level.

Model	Deviance	no. Estim	d.f.	Over-dispersion	nullΔdev	AIC	ΔAIC
CRS $CSTb_{t=-2}$	148.46	7	35	4.24	6.44*	162.46	0.00
GAM $CSTb_{t=-5}$	149.51	7	35	4.27	5.39*	163.51	1.05
CRS $climate_{t=-2}$	147.85	8	34	4.35	7.05*	163.85	1.39
GAM $CSTb_{t=-4}$	150.29	7	35	4.29	4.61*	164.29	1.82
GAM $climate_{t=-5}$	149.05	8	34	4.38	5.85*	165.05	2.59
GAM $CSTb_{t=-2}$	151.55	7	35	4.33	3.35	165.55	3.09
GAM $climate_{t=-4}$	150.22	8	34	4.42	4.68	166.22	3.76
CRS $climate_{t=-5}$	152.35	8	34	4.48	2.55	166.30	3.84
CRS $CSTnb_{t=-3}$	152.83	7	35	4.37	2.07	166.83	4.37
Null	154.90	6	36	4.30		166.97	4.50
CRS $climate_{t=-3}$	151.22	8	34	4.45	3.68	167.22	4.76
CRS $CSTnb_{t=-4}$	153.23	7	35	4.38	1.67	167.23	4.77
CRS $CSTb_{t=-3}$	153.39	7	35	4.38	1.51	167.39	4.93
CRS $climate_{t=-4}$	151.40	8	34	4.45	3.50	167.41	4.95
CRS $CSTb_{t=-4}$	153.49	7	35	4.39	1.41	167.50	5.04
GAM $climate_{t=-2}$	151.54	8	34	4.46	3.36	167.54	5.08
CRS $CSTnb_{t=-2}$	153.58	7	35	4.39	1.32	167.59	5.13
CRS $CSTnb_{t=-5}$	153.78	7	35	4.39	1.12	167.78	5.32
GAM $CSTnb_{t=-3}$	153.78	7	35	4.39	1.12	167.78	5.32
GAM $CSTnb_{t=-2}$	154.34	7	35	4.41	0.56	168.34	5.87
GAM $CSTnb_{t=-4}$	154.42	7	35	4.41	0.48	168.42	5.96
GAM $CSTb_{t=-3}$	154.46	7	35	4.41	0.44	168.46	6.00
CRS $CSTb_{t=-5}$	154.72	7	35	4.42	0.18	168.70	6.24
GAM $CSTnb_{t=-5}$	154.99	7	35	4.43	-0.09	168.99	6.53
GAM $climate_{t=-3}$	153.56	8	34	4.52	1.35	169.56	7.09

Passerines

Models that were retained for the 1970-1990 data included either breeding and non-breeding climate trends together or alone along with habitat (Table 5.20). Log-likelihood tests revealed that GAM and CRS climatic models were not significantly different. AIC model selection showed that the best model was habitat plus GAM CSTnb with a two-year time lag (Table 5.20). Analyses of residual deviance confirmed that these models were different from the null model. However, all models were not significantly better than the null model when correcting for over-dispersion.

Table 5.20: Ordinal regression statistics for Passerines with 1970-1990 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model. * denotes significance at the 0.05 level.

Model	Deviance	no. Estim	d.f.	Over-dispersion	NullΔdev	AIC	ΔAIC
Base + GAM $CSTnb_{t = -2}$	133.20	9	49	2.72	12.04*	149.20	0.00
Base (Habitat)	136.06	8	50	2.72	9.18*	150.09	0.89
Base + CRS $CSTnb_{t = -2}$	134.40	9	49	2.74	10.84*	150.40	1.20
Base + GAM $CSTnb_{t = -1}$	134.50	9	49	2.74	10.74*	150.50	1.30
Base + CRS $CSTnb_{t = -1}$	134.61	9	49	2.75	10.63	150.61	1.41
Base + GAM $climate_{t = -2}$	132.72	10	48	2.77	12.52*	150.72	1.52
Base + GAM $CSTnb_{t = 0}$	134.81	9	49	2.75	10.43	150.81	1.61
Base + CRS $CSTb_{t = -2}$	135.00	9	49	2.76	10.24	151.00	1.80
Base + GAM $CSTb_{t = -1}$ + $CSTnb_{t = -2}$	133.03	10	48	2.77	12.21*	151.03	1.83
Base + CRS $CSTb_{t = -1}$	135.21	9	49	2.76	10.03	151.21	2.01
Null	145.24	4	54	2.69		151.24	2.04
Base + CRS $climate_{t = -2}$	133.32	10	48	2.78	11.92	151.32	2.12
Base + CRS $CSTnb_{t = 0}$	135.53	9	49	2.77	9.71	151.53	2.33
Base + CRS $CSTb_{t = -1}$ + $CSTnb_{t = -2}$	133.54	10	48	2.78	11.70	151.54	2.34
Base + CRS $CSTb_{t = 0}$	135.84	9	49	2.77	9.40	151.84	2.64
Base + CRS $climate_{t = -1}$	133.84	10	48	2.79	11.40	151.84	2.64
Base + GAM $CSTb_{t = -2}$	135.95	9	49	2.77	9.29	151.95	2.75
Base + GAM $CSTb_{t = -1}$	136.04	9	49	2.78	9.20	152.04	2.84
Base + GAM $CSTb_{t = 0}$	136.08	9	49	2.78	9.16	152.08	2.88
Base + GAM $climate_{t = -1}$	134.25	10	48	2.80	10.99	152.25	3.05
Base + CRS $CSTb_{t = 0}$ + $CSTnb_{t = -1}$	134.32	10	48	2.80	10.92	152.32	3.12
Base + GAM $CSb_{t = 0}$ + $CSTnb_{t = -1}$	134.49	10	48	2.80	10.75	152.48	3.28
Base + GAM $climate_{t = 0}$	134.83	10	48	2.81	10.41	152.83	3.63
Base + CRS $climate_{t = 0}$	135.41	10	48	2.82	9.83	153.41	4.21

There was a non-significant positive correlation between breeding CST with a two-year time lag and population trend (Fig. 5.16a; Spearman rho = 0.04, p=0.738) but a significant negative correlation between non-breeding CST with a two-year time lag and population trend (Fig. 5.16b; Spearman rho = -0.38, p<0.01).

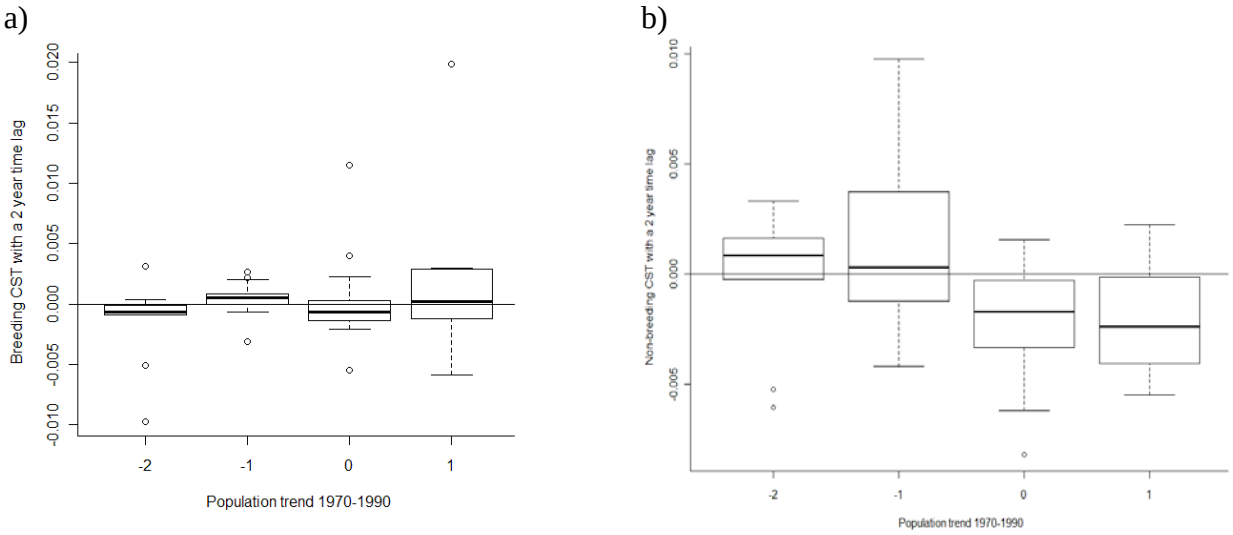


Figure 5.16: Passerines' population trend during the 1970-1990 period and Climate Suitability Trend; a) GAM breeding CST with a two-year time lag; b) GAM non-breeding CST with a two-year time lag.

Table A29 details each species' individual climatic suitability trend. This shows how weak the trends are. Twenty-two species have significant CSTnb and four species have significant CSTb. This is much greater than non-passerine CST significance.

Models that were retained for the 1990-2000 data included either both breeding and non-breeding climate trends together or alone (Table 5.21). Log-likelihood tests revealed that GAM and CRS climatic models were not significantly different.

AIC model selection showed that the best model was GAM CSTnb with a one-year time lag, closely followed by GAM climate with a two-year time lag (Table 5.21). Analyses of residual deviance showed, however, that the model consisting of GAM climate with a two-year time lag was the best. Analyses of residual deviance confirmed that these models are different from the null model. However, all models were not significantly better than the null model when correcting for over-dispersion.

Table 5.21: Ordinal regression statistics for Passerines with 1990-2000 population trend as the response variable. CRS = Climate Response Surface; GAM = Generalised Additive Models; b = breeding; nb = non-breeding; CST = climate suitability trend; climate = CSTb+CSTnb; NullΔdev is the difference in deviance with the null model.

Model	Deviance	no. Estim	d.f.	Over-dispersion	NullΔdev	AIC	ΔAIC
GAM $CSTnb_{t=-1}$	237.32	7	76	3.12	5.22*	251.32	0.00
GAM $climate_{t=-2}$	235.71	8	75	3.14	6.83*	251.71	0.39
GAM $CSTnb_{t=-2}$	238.02	7	76	3.13	4.52*	252.02	0.70
GAM $climate_{t=-1}$	236.63	8	75	3.16	5.91*	252.63	1.31
GAM $CSTb_{t=0}$+ $CSTnb_{t=-1}$	236.64	8	75	3.16	5.90*	252.64	1.32
GAM $CSTb_{t=-1}$+ $CSTnb_{t=-2}$	237.32	8	75	3.16	5.22*	253.32	2.00
CRS $CSTnb_{t=-1}$	239.88	7	76	3.16	2.66	253.88	2.56
CRS $CSTnb_{t=-2}$	239.96	7	76	3.16	2.58	253.96	2.64
CRS $CSTb_{t=0}$+ $CSTnb_{t=-1}$	238.52	8	75	3.18	4.02	254.52	3.20
Null	242.54	6	77	3.15		254.54	3.22
CRS $climate_{t=-1}$	239.02	8	75	3.19	3.52	255.02	3.70
CRS $CSTb_{t=-1}$+ $CSTnb_{t=-2}$	239.28	8	75	3.19	3.26	255.28	3.96
CRS $climate_{t=-2}$	239.59	8	75	3.19	2.95	255.59	4.27
GAM $CSTnb_{t=0}$	241.75	7	76	3.18	0.79	255.75	4.43
CRS $CSTnb_{t=0}$	241.77	7	76	3.18	0.77	255.77	4.45
GAM $CSTb_{t=-2}$	242.35	7	76	3.19	0.19	256.35	5.03
CRS $CSTb_{t=0}$	242.40	7	76	3.19	0.14	256.4	5.08
CRS $CSTb_{t=-1}$	242.51	7	76	3.19	0.03	256.51	5.19
CRS $CSTb_{t=-2}$	242.52	7	76	3.19	0.02	256.52	5.20
GAM $CSTb_{t=0}$	242.54	7	76	3.19	0.00	256.54	5.22
GAM $CSTb_{t=-1}$	242.54	7	76	3.19	0.00	256.54	5.22
CRS $climate_{t=0}$	241.32	8	75	3.22	1.22	257.32	6.00
GAM $climate_{t=0}$	241.72	8	75	3.22	0.82	257.72	6.40

Figure 5.17 shows GAM CSTb with a two-year time lag (Fig.5.17a) and GAM CSTnb with a two-year time lag (Fig.5.17b) for the 1990-2000 population trends. Fig. 5.17a suggests that, despite considerable variation, there is a positive relationship between breeding CST and population trend. The population trend category 3 has only one species (*Carpospiza brachydactyla*) and so cannot be counted as representative. However, the positive correlation was not significant (Spearman correlation minus that one species: rho = 0.02; p = 0.84). There was a significant negative relationship between non-breeding CST and population trend (Fig. 5.17b; Spearman rho = -0.27, p < 0.05).

a) b)

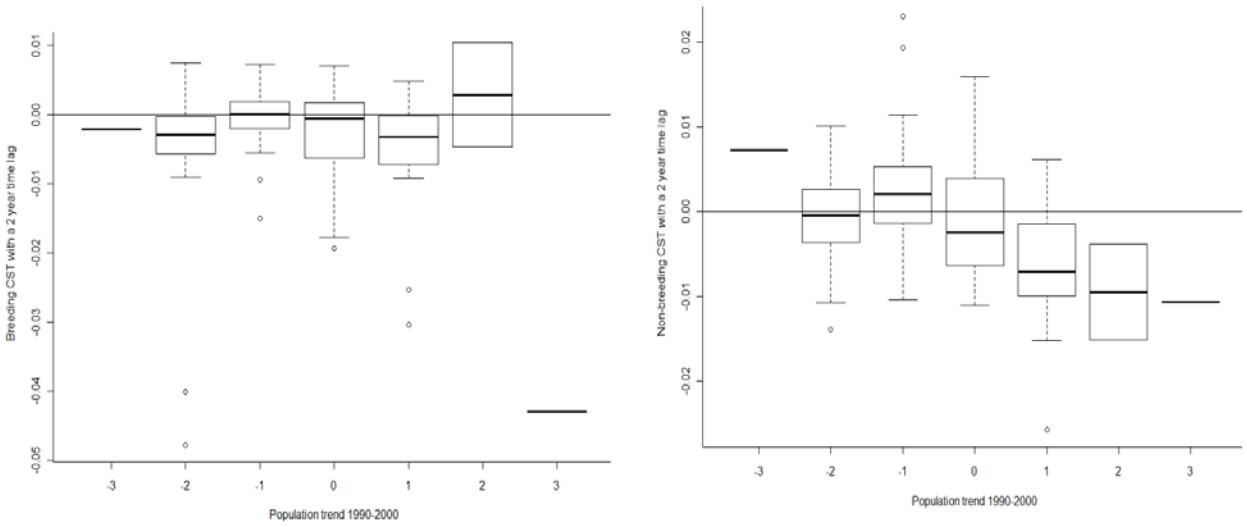


Figure 5.17: Passerine population trend during the 1990-2000 period and Climate Suitability Trend (CST) as modeled by GAM with a 2-year time lag; a) breeding CST and b) non-breeding CST.

Table A29 details each species' individual climatic suitability trend. This shows how weak the trends are. Twelve species had significant CSTnb. Four decreasing species' populations had negative CST, while five increasing populations had negative CST. The remaining three species had stable population trends. Six species had significant CSTb, four of which had stable populations; the remaining two had negative CST and decreasing populations.

5.2.4 Discussion

The climate suitability trends (CST) derived from the GAM and CRS models were very similar, and in most case produced models that were not significantly different in their predictions. GAM CST was, nevertheless, more often a better fitting model than CRS CST in terms of AIC at least. The CST calculated were very weak (Tables A27-29) and hid much of the annual variation. This was also the case for the trends calculated by Green *et al.* (2008) and Gregory *et al.* (2009). Gregory *et al.* (2007) found significant correlations between population trend and winter weather for only five out of 18 species. My results indicate that passerine species had more significant trends than non-passerine species.

My results show that for all species, species' grouping (passerine or non-passerine) was an important factor in determining population trends. Bauer *et al.* (2008) found that there were diverging trends in passerine and non-passerine species richness in central Europe between 1980-1990 and 1990-2000. The differences were probably due to differences in body size, habitats and migratory strategies. Habitat was found to be an important factor in population trends during the 1970-1990 period. In the separate analyses of passerines and non-passerines, only passerines were affected by their habitat characteristics. It is not surprising that habitat should be important during that time period because the European landscape was changing rapidly (Chamberlain *et al.*, 2000; Fuller *et al.*, 2007; Fuller and Ausden, 2008; Dallimer *et al.*, 2009) and agricultural intensification led to many bird population declines (Newton, 2004). Migratory strategy was also found to be a factor in the analyses of population trends of all species for 1990-2000. Long-distance migrants were found to decline more on average than the other groups. These results are comparable to the findings of Sanderson *et al.* (2006) and Gregory *et al.*(2007).

In the analyses separating non-passerines into early/late breeders, the results showed that better models could be constructed for the earlier breeders. This is not surprising since species with later broods tend to be of larger body size, longer-lived and hence prone to different pressures such as persecution and demographic effects (Pimm *et al.*, 1988). Non-breeding biome was found to improve the models for early breeding non-passerine species. Furthermore, either both breeding and non-breeding CST (1970-1990) or non-breeding CST (for 1990-2000) affected these species. For late breeding non-passerine species, breeding CST was highlighted as the best explanatory climatic variable. For passerine species, non-breeding CST was chosen in both time periods. There has been some debate on whether the "tap or tub" hypothesis regulates bird population densities. In the tap-hypothesis, annual survivorship is determined by (weather)

conditions on the breeding grounds, while in the tub-hypothesis population size is regulated by conditions during the non-breeding season in combination with density-dependence (Saether *et al*., 2004). The literature points to both hypotheses having support, though there are some general trends. In particular, a review by Saether *et al.* (2004) found that northern temperate altrical bird populations seem to be influenced by weather during the non-breeding season, while many nidifugous species, species that leave the nest shortly after hatching, as well as those residing in arid conditions are affected by conditions during the breeding season. The analysis done here is not powerful enough, however, to provide support for any of these hypotheses due to the coarse nature of the analysis (see below). It may be that dividing the species into the broad groups according to the findings of Sather *et al.* (2004) improves the models (but see below).

The ordinal models produced for the 1970-1990 period were better than for the 1990-2000 period as shown by larger over-dispersion in the models for the latter time frame. It is possible that the second time period is too short for effects on populations to be discerned. However, the over-dispersion in all the models was large suggesting that either the variables are not important, or some other important factor(s) has/have been excluded. Studies examining factors impacting on species' demography, have found that although climate is important, the majority of the variation in population size could be explained by density-dependence (Ådahl *et al.*, 2006; Beale *et al.*, 2006; Pellet *et al.*, 2006; Holmes, 2007). Pellet *et al.* (2006) evaluated the relative importance of intrinsic density-dependence and extrinsic factors, such as weather, either alone or in combination, for population growth. They used a 22 year time series of an isolated population of *Hyla arborea* that was not declining. They found that density-dependence alone explained the majority of the variance in the models. However, the best model also included rainfall with a two-year time lag. They concluded that density dependence affects population growth rate directly but that it also acts in combination with lagged climatic variables. Density dependence is also important in bird populations. Holmes' (2007) review of factors affecting migratory bird abundances revealed that abundances of migratory passerines on their temperate breeding grounds are regulated by density-dependent fecundity. Fecundity is regulated in turn by various other factors including weather-induced food limitation. However, density-dependence is unlikely to explain the absence of relationship between climate and population trends or be the factor explaining long-term population trends.

My results also indicated time lagged climatic effects. For non-passerines, the results indicated a significant positive correlation between breeding CST with a four-year time lag and population trend during the 1970-1990 period. Separating non-passerines in that period revealed a

four- to five-year lag for both groups in concurrence with the analyses for all non-passerines during that time frame. There was no significant correlation between population trend and climate during the 1990-2000 period, although model selection indicated that models including breeding CST and a five-year time lag were best. The non-significant relationship may be an artefact of the large variation between 'best' models. For early breeding non-passerines, a three-year time lagged climate model was selected, followed by a one-year lagged CST. For late breeding non-passerines, two-, five- and four-year time lagged CST models were selected. The presence of large time lags for non-passerines may be due either to the time of reproductive maturity (Thompson and Ollason, 2001) or to an indirect climatic lagged effect on these species. For instance, habitat may be affected by a series of bad years, which may in turn affect the food source (Sandvik *et al.*, 2008), which eventually affects bird populations.

For passerine species, a two-year time lag in CST was found in both periods. Furthermore, model selection suggested that non-breeding CST or the combination of both breeding and non-breeding CST was important. Breeding CST showed non-significant positive correlations with population trends, while non-breeding CST was significantly negatively correlated with population trend. Gregory *et al.* (2009) found a near significant positive correlation ($p = 0.05$) between CST and population trend when confounding variables were accounted for, otherwise the correlation was not significant.

The significant negative correlation with non-breeding CST is surprising. However, there are a number of possible explanations. First, if increased climate suitability on the non-breeding grounds equates to more favourable climate in general, then competition between resident and migratory birds may be increased (Bohning-Gaese and Lemoine, 2004). Suttle *et al.* (2007) showed that species interactions could reverse the expected outcome of climate change in their experiment of species diversity in grassland plots. Moreover, a negative relationship between long-term bird population trends and productivity has been observed (Siriwarden *et al.*, 2000). Second, disease may be increased in favourable climates (McCarty, 2001). Third, there may also be a confounding effect of land-use. Areas that are more climatically favourable may also be areas with high human disturbance, thus impacting on bird abundance. Fourth, the combined effects of changes in CST on the breeding grounds and non-breeding grounds, may act in a non-linear way. Changes in leaving and arrival dates in migratory species may interact with changes in CST, leading to changes in cohort size due to competition for territories or an asynchrony between arrival to the breeding grounds and insect emergence (see Chapter 2). Fifth, decreased abundance in opposition to improved climate is a signal of range expansion. Monahan and

Hijmans (2008) found that for *Spizella pusilla*, as the non-breeding range expanded polewards between 1940 and 1997, population abundance appeared to decrease, because the species occupied new sites further north where it had never occurred before and, hence, was not monitored.

Chi-square tests showed that inclusion of climate as an explanatory variable significantly improved the fit of the models for many species for the 1970-1990 data sets. For 1990-2000, the models utilising climate increased the proportion of correctly predicted trends, compared with the null model, but the models were not significantly different from the null model. Eleven species' trends (8%) for the 1970-1990 period and twenty-one species' trends (11%) for the 1990-2000 period were wrongly predicted. The models indicated that these species should decline, even though they fact increased. Conservation measures or improved habitat might account for these changes which over-ride climate effects. Okes *et al.* (2008) showed that human-mediated habitat change was more of an influential driver in water bird range change in South Africa than climate change. Anthropogenic changes in land-use may, therefore, over-ride the natural indirect effects of climate change for some species. Other extrinsic factors may also be more important in determining population trends during the two time periods, such as hunting pressure, land-use change or conservation efforts.

Overall, my results suggest that, despite the coarseness of the data, there is a detectable climate signal, albeit weak, in the population trends. The weak signal may be in part due to the fact that climate has not changed markedly over the time-scale analysed. Moreover, the climate trends hide the huge inter-annual variability. Population-climate relationships might be better examined by taking the inter-annual trends into account. Furthermore, noticeable changes in species' abundance may be more influenced by extreme climatic events. Indeed, Newton (2007) reports unseasonal weather incidents causing reductions in population size which may take several years to recover.

McRae *et al.* (2008) also found a disparity between population numbers and habitat suitability. They constructed a framework of models to predict wildlife population trends in response to habitat and climate change. Their results indicated that population trends changed more than their habitat suitability indices. Furthermore, their results indicated that, although climate change impacts habitat, it had negligible consequences for simulated bird populations (McRae *et al.*, 2008). Another possibility is that fluctuations or extreme events were modelled by the climate envelope models (CEM), and that these biased the CST values. Gregory *et al.* (2009) state that, "as calculated, CST is sensitive to extreme annual values of meteorological variables

and often has relatively low precision as a result" (p.4); they suggest, therefore, that this might be a cause for the poor correlation with bird trends.

Green *et al.* (2008) found a positive correlation between breeding bird trends in the UK and CST. Their study was conducted at the edge of birds' ranges, and was fine-scale enough to exclude species that were known to have declined in the UK due to persecution. Comparison with the results of this study indicates that my models may be too coarse to detect a clear signal. Climate affects species differently at the range centre versus the edge of range (Jarema *et al.*, 2009), as well as differently between the leading and trailing edge (Foden *et al.*, 2007); furthermore, species are not evenly distributed within their ranges (Lawton, 1993). Bird population trends vary widely across Europe (Tucker *et al.*, 1997; Birdlife International, 2004) and trends in different parts of Europe may be affected by different mechanisms. Moreover, average population trends may not necessarily match average climate suitability because population trends were weighted according to population size (Tucker *et al.*, 1997; Birdlife International, 2004), whereas average CST takes into account the entire study area equally.

Overall pan-European population trends hide much of the variation in population trends across Europe. Analysing population trends and climate suitability by region or countries may be more revealing in terms of the strength of the relationship between climate and population trends (Appendix III d). Foreseeable problems with this are that, first, the quality of population trend data varies across Europe. Second, information about where species from different countries spend their non-breeding seasons, is severely deficient and, for some species, conditions on the non-breeding grounds are known to be important. Third, different processes have affected species in different parts of their range, such as differing land-use on an East-West basis across Europe. Fourth, at finer scales, current research has shown that land cover (Pearson and Dawson, 2003; Pearson, *et al.* 2004; Thuiller *et al.*, 2004; Luoto *et al.*, 2007) and biotic interactions (Heikkinen *et al.*, 2007) become important. Finally, demographic factors, as well as past population trends, are still likely to account for much of the fluctuation in population size. Results presented in Appendix III d show that, for some species, there is a (clear) climate signal underlying population change. However, there is still much unexplained variance in the data set confirming the above reservations and the conclusions from the analysis presented in this section.

A note of caution on the analyses undertaken in this section is the possible over-interpretation of my results. Indeed multiple-hypothesis testing, testing at the same time many different models and many species, will greatly increase the likelihood of false positive results (Whittingham *et al.*, 2006; Mundry and Nunn, 2009). This means that the relationship between

climatic trends and population trends, as shown by my results, is uncertain and warrants further research.

5.2.5 Conclusion

Despite the use of coarse scale data and the limitations of this study, the results of my study are encouraging in the light of Green *et al.* (2008) and Gregory *et al*. (2009) studies. Together, our results indicate that CEM are modelling relevant changes in climate that are affecting species to some degree. The assessment of the effect of climate on populations is rendered difficult by the weak climatic trends during the time periods considered. Future climate change is predicted to be more dramatic and, therefore, a more direct link between climatic suitability and population numbers may be seen. Moreover, palaeoecological evidence suggests that species' numbers have changed due to climate mediated range contraction (Lister and Stuart, 2008). I would, however, use caution when inferring changes in population numbers solely from CEMs because species' numbers are affected by factors other than climate, as my results show.

Indeed, the models depicting population trends are clearly missing some important factor(s). Nest predation, breeding success (Holmes, 2007), competition (Lemoine and Böhning-Gaese, 2003), and weather[3] (Newton, 2006) have been shown to affect population size. Furthermore, migratory birds are also affected by factors in between their breeding and non-breeding grounds, which were not taken into account. Changes along the migratory route can be very important in terms of survivorship (Newton, 2006). Holmes (2007) reported that 85% of apparent annual mortality of the migratory *Dendroica caerulescens* occurred during migration rather than during the stationary periods. Adequate habitat areas, food supply and weather conditions all affect species' migration (see Chapter 2).

The effect of climate change on bird populations may not necessarily be direct. Climate may impact on species' food sources (Both *et al.*, 2006; Holmes, 2007; Sandvik *et al.*, 2008) or change habitat quality (Treinys *et al.*, 2008). Changes due to climate in arrival time onto the breeding/non-breeding grounds may also affect species (Both *et al.*, 2006). Furthermore, population responses to direct and indirect effects of climate change may not be linear due to demographic regulation and density-dependence (Ådahl *et al.*, 2006; Holmes, 2007). More research is needed into how climate influences population abundances.

[3] Weather is not the same as climate (see page 7).

5.3 Populations' vulnerability to climatic change

5.3.1 Introduction

The previous section linked past population changes to average change in climate suitability during the same period. The results showed a weak association between climate and population change. Other factors confound the effects of climatic change and studies indicate that populations may respond to climatic change in a complex manner (Ådahl *et al.*, 2006; Holmes, 2007; Suttle *et al.*, 2007).

Future changes in climate are projected to be more dramatic than in the past (IPCC, 2007), so future population change may more clearly be linked to climate. However, distinguishing between climatic effects and other effects on population numbers may still be difficult unless there is a direct change in mortality/survivorship or fecundity. Indirect effects may be much slower to operate due to lags in the system and, hence, may not correlate well with recorded climatic changes. Changes in species' ranges appear to be attributable to climatic change more than to population changes. Human-induced range changes not relating to climate, such as from habitat alteration (Okes *et al.*, 2008), have also been observed.

Although the link between population size and range size is not necessarily straightforward (Lawton, 1993), it is agreed that changes in range, whether due to contraction or fragmentation, must (eventually) have an impact on species' numbers (IUCN, 2001; Lister and Stuart, 2008), though not necessarily on extinction risk (Shoo *et al.*, 2005a; Akçakaya *et al.*, 2006). Shoo *et al*. (2005a) examined the extinction risk of rainforest birds in Australia. They found that species varied in their response (population trajectory) to increasing temperature and had lower extinction rates that those reported from similar studies using changes in range size.

Species have already started to adjust their ranges due to climatic change (Parmesan and Yohe, 2003) though some studies report a lag in this adjustment (Menendez *et al.*, 2006; Devictor *et al.*, 2008). Many studies, including my results, have found lagged population responses to climate (see previous section). Population responses may, moreover, change at a different rate to range size. Shoo *et al.* (2005b) showed that decreases in population size can occur at a faster rate than decline in range size. Rhodes *et al.* (2008) suggest that species may exhibit threshold responses to habitat loss and, furthermore, that the threshold may vary across a species' range.

Alternatively, population responses to current subtle changes in climate may not be detectable in the present time period though their trajectory may tend in the direction of projected change. Moreover, as climate change has been more pronounced in the latter part of the 20th century and beginning of 21st century than previously (Dore, 2005), population trends covering this latter time-frame may exhibit a clear climatic signal. Gregory *et al.* (2009) found that future climate change projections matched current population trends. They found a significant positive relationship between observed bird population trends and the projection of change in species' range extent. They used this as a basis for an indicator of climate change effects on species. However, migratory birds are subject to changes not only on their breeding and non-breeding ranges but also to changes in migratory distance. I, therefore, used both breeding and non-breeding range changes to produce an index of impact of climate change (section 5.1). In this section, I explore the relationship between recent population change and future climate change vulnerability. If climate has been a strong driver of recent population change, I would expect a negative relationship between population change and species' vulnerability categorisation (see below). However, as discussed in the previous section, the effects of climate change may not necessarily be direct or may be overwhelmed by other factors. This indicates that I may not find an association between climate and population trend.

5.3.2 Methods

The Vulnerability index outlined in section 5.1 is a pressure index in that it always has a negative connotation, going from least vulnerable to extremely vulnerable. To account for this, the positive measures of population change were coded into one category so that "stable" to "increasing" population trend categories were coded as 0. The other categories were coded in the same way as in section 5.2. Vulnerability categories were coded as 1 = least vulnerable, 2 = moderately vulnerable, 3 = vulnerable, 4 = highly vulnerable and 5 = extremely vulnerable (see section 5.1).

The degree of correspondence between population trends (for the periods 1970-1990 and 1990-2000) and future climate change sensitivity, as determined by each species' Vulnerability category (see section 5.1) was measured using Kendall's τ test. Kendall's τ has values ranging from -1 (100% negative association) to $+1$ (100% positive association). A value of zero indicates the absence of association (SPSS Inc., 2006). Migratory strategy, species' grouping (passerine and non-passerine) and habitat (see Table 3.15) were taken into account for this test because

these factors were shown to be important for those two measures (see sections 5.1 and 5.2). The analysis was done separately and in combination. Non-passerines were not further split into early/late breeders as there were not enough species in each habitat category to give reliable results.

Species in the extremely vulnerable category (see Tables 5.3-5.5 and A24-26) were examined using Chi-square tests to see if current population trends were more likely to be decreasing than increasing or having a stable population. In order to do so, species were assigned an increasing, stable or decreasing category if the population trend was consistent through both time periods. Species with differing trends (34 species in total – see table A27-29) were excluded for the analysis

5.3.3 Results

Analysis of correspondence between the 1970-1990 population trends and future Vulnerability category for the A1B scenario is shown in Tables 5.22 and 5.23 and in table A30 and A31 for the A2 scenario, which gives similar results. There was no significant association between Vulnerability category and population trend for European and trans-Saharan migrants, meaning that there was no significant difference in the distribution of Vscores among species' trends (Table 5.22). However, split strategy migrants had a positive association with the 2025 and 2055 index. This indicates that currently stable/increasing populations are projected to be at greater risk from future climatic change than currently declining populations.

Table 5.22: Analysis of correspondence between the 1970-1990 population trends of the different migratory groups and future Vulnerability category according to the A1B scenario. N is the number of species in each category.

		2025		2055		2085	
Species	N	Kendall τ	p	Kendall τ	p	Kendall τ	p
European	26	0.071	0.389	0.008	0.938	-0.158	0.217
Split-strategy	55	0.285	0.007	0.289	0.010	0.178	0.120
Trans-Saharan	51	-0.138	0.220	-0.103	0.360	0.078	0.524

Table 5.23 shows that upland species had a strong negative association between Vulnerability category and population trend. Splitting into passerines and non-passerines revealed no association between population trend and the index for passerine species. For non-passerines, forest species had a significant negative association with the 2085 index. This means that

declining species have a tendency to have higher Vscores than stable/increasing species. However, sample sizes were small in some cases (Table 5.23), which may result in unreliable results (Hill and Lewick, 2005).

Table 5.23: Analysis of correspondence between the 1970-1990 population trends and future Vulnerability category by habitat according to the A1B scenario. N is the number of species in each category.

		2025		2055		2085	
All Species	N	Kendall τ	p	Kendall τ	p	Kendall τ	p
Open habitat	36	0.138	0.329	0.158	0.250	0.165	0.216
Forest	37	-0.018	0.854	-0.117	0.209	-0.127	0.298
Upland	7	-0.544	0.005	-0.762	0.000	-0.367	0.178
Wetland	25	0.119	0.394	0.273	0.034	0.222	0.115
Passerine							
Open habitat	15	0.160	0.551	0.173	0.475	0.240	0.169
Forest	27	0.033	0.818	-0.041	0.772	-0.078	0.582
Upland	3	0.000	1.000	0.000	1.000	-0.444	0.221
Wetland	3	0.444	0.221	0.444	0.221	0.444	0.221
Scrub	15	-0.187	0.387	-0.080	0.707	-0.187	0.345
Non-passerine							
Open habitat	21	0.211	0.217	0.218	0.186	0.231	0.173
Forest	10	-0.090	0.765	-0.210	0.501	-0.450	0.041
Upland	4	-0.750	0.083	-0.750	0.083	-0.250	0.317
Wetland	22	0.105	0.559	0.341	0.048	0.260	0.139
Coastal	11	0.372	0.242	0.198	0.547	0.149	0.591

Analysis of correspondence between the 1990-2000 population trends and future Vulnerability category for the A1B scenario showed no linear trend among the different migratory categories (Table 5.24).

Table 5.24: Analysis of correspondence between the 1990-2000 population trends of the different migratory groups and future Vulnerability category according to the A1B scenario. N is the number of species in each category.

		2025		2055		2085	
Species	N	Kendall τ	p	Kendall τ	p	Kendall τ	p
European	40	0.033	0.725	0.053	0.646	-0.033	0.776
Split-strategy	91	0.112	0.128	0.109	0.203	0.082	0.325
Trans-Saharan	65	-0.078	0.444	-0.115	0.206	-0.015	0.876

Upland species showed a significant negative relationship between their sensitivity to future climate change and current population trend (Table 5.25). For passerine species, forest dwellers had a significant negative association between population trend and vulnerability category (Table 5.25).

Table 5.25: Analysis of correspondence between the 1990-2000 population trends and future Vulnerability category by habitat according to the A1B scenario. N is the number of species in each category.

		2025		2055		2085	
All Species	N	Kendall τ	p	Kendall τ	p	Kendall τ	p
Open habitat	50	0.001	0.993	0.059	0.632	0.140	0.238
Forest	49	-0.086	0.443	-0.135	0.276	-0.191	0.101
Upland	13	-0.503	0.000	-0.473	0.036	-0.205	0.420
Wetland	45	0.100	0.341	0.058	0.596	-0.014	0.902
Passerine							
Open habitat	21	-0.020	0.909	0.042	0.825	0.075	0.557
Forest	35	-0.269	0.032	-0.274	0.040	-0.313	0.020
Upland	8	-0.375	0.131	-0.234	0.388	-0.188	0.433
Wetland	7	0.490	0.003	0.367	0.173	0.306	0.324
Scrub	16	0.035	0.872	-0.082	0.704	-0.188	0.380
Non-passerine							
Open habitat	29	0.117	0.462	0.120	0.465	0.212	0.141
Forest	14	0.184	0.309	0.153	0.407	0.015	0.949
Upland	5	-0.720	0.000	-0.960	0.000	-0.360	0.312
Wetland	38	0.102	0.425	0.079	0.531	0.015	0.909
Coastal	18	0.165	0.282	0.132	0.424	0.198	0.238

Table 5.26 shows species with consistent trends throughout the 1960-2000 period that are classified as extremely vulnerable to future climate change. Although in each time period the majority of species' population trends are either decreasing or stable, there was no significant difference in the number of decreasing, stable or increasing species (A1B scenario: for 2025 $\chi^2_2 = 1.6$, p=0.449; for 2055 $\chi^2_2 = 1.6$, p=0.449; for 2085 $\chi^2_2 = 0.25$, p=0.882. A2 scenario: for 2025 $\chi^2_2 = 1$, p=0.606; for 2055 $\chi^2_2 = 0.4$, p=0.818; for 2085 $\chi^2_2 = 1.75$, p=0.416).

Table 5.26: Species and population trend for the 1960-2000 period in the extremely vulnerable to climate change category for three time periods of the A1B scenario

2025	*Anas penelope*	stable
	Apus affinis	decreasing
	Bubulcus ibis	increasing
	Charadrius morinellus	decreasing
	Chlidonais hybridus	increasing
	Egretta alba	increasing
	Falco columbarius	stable
	Milvus migrans	decreasing
	Neophron percnopterus	decreasing
	Oenanthe xanthoprymna	decreasing
	Pelecanus onocrotatus	stable
	Porzana parva	decreasing
	Sterna sandvicensis	decreasing
	Tachybaptus ruficollis	stable
	Turdus torquatus	stable
2055	*Anas penelope*	stable
	Apus affinis	decreasing
	Bubulcus ibis	increasing
	Carpospiza brachydactyla	increasing
	Charadrius morinellus	decreasing
	Chlidonais hybridus	increasing
	Egretta alba	increasing
	Lymnocryptes minimus	decreasing
	Melanocorypha bimaculata	increasing
	Neophron percnopterus	decreasing
	Oenanthe xanthoprymna	decreasing
	Pelecanus onocrotatus	stable
	Porzana parva	decreasing
	Sterna sandvicensis	decreasing
	Tachybaptus ruficollis	stable
2085	*Calidris minuta*	stable
	Calidris temminckii	stable
	Chlidonais hybridus	increasing
	Lymnocryptes minimus	decreasing
	Melanocorypha bimaculata	increasing
	Porzana parva	decreasing
	Sterna sandvicensis	decreasing
	Sylvia sarda	stable

5.3.4 Discussion

The results show that for the majority of cases there is no significant association between current population trends and species' sensitivity to future climatic change. This result is not particularly surprising because the data and analyses used were much coarser than those used by Gregory *et al*. (2009). However, my results show some significant negative associations. Separating species into migratory category did not reveal any significant associations except for split-strategy migrants. This suggests that either other factors than climate are important in shaping these species' population trends or that climatic effects are interacting with other factors producing complex responses (see Shuttle *et al.*, 2007). Interestingly, Kendall's τ for trans-Saharan migrants was nearly always negative. Trans-Saharan migrants are generally declining and climate change has been suggested as a potential driver (Sanderson *et al.*, 2006). The non-significant association, however, suggests that climate may be a driver for some but not all species.

For passerine species inhabiting forest and upland, currently declining populations were more likely to be classified as at higher risk from climate change than increasing populations. This indicates that, for some of these species, climate may be an important factor underlying their population changes. Furthermore, the results presented in Appendix III d show that, for individual species, clear climatic signals can be found. These results indicate that the underlying causes of population fluctuations are species-specific rather than general and suggest that future research should concentrate on species-specific investigations including all relevant and confounding factors (see section 5.2.4).

Gregory *et al.* (2007) examined population changes across Europe among forest birds during 1980-2003 and found that common forest birds had declined by 13% and forest specialists by 18%. Among these species, long-distance migrants and resident species were more likely to be declining than partial migrants. However, Gregory *et al.* (2007) found that nest type was the only significant explanatory variable. They also examined whether winter weather was associated with population trends and, although there was a weak correlation between the two, the correlation was only significant for five species. My analysis, however, takes into account potential changes in range extent, range conservatism and migratory distance. The results presented in section 5.1 indicated that forest species were more likely to be assigned their position in the sensitivity index due to contracting ranges and greater future migratory distance. *Muscicapa striata*, *Ficedula hypoleuca* and *Sylvia hortensis* are examples of forest species currently declining and classified

as either “Vulnerable” or “highly Vulnerable” to climatic change. English Nature (1998) suggests that *Muscicapa striata* is declining due to climatic factors or changes in agricultural practice and loss of nest sites. It has been suggested that *Ficedula hypoleuca* declines are due to climate induced phenological mis-matching (Both *et al.*, 2006). The species’ climate sensitivities, along with the possibilities that current declines are climate-related, suggest that climate is a driver in these species declines.

Both Gregory *et al.* (2007) and BirdLife International (2004) indicate that birds primarily associated with boreal and temperate forests are declining. My results, however, suggest that many southern-biased species should be vulnerable to climate change (Tables 5.3-5.5 and A24-26). However, if their projected distributional change is due to future water limitation, changes in distribution or population declines may not take place (and may not be currently experienced) due to human intervention (Böhning-Gaese and Lemoine, 2004). Declining northern populations could be climate induced since climate change projections indicate that many species’ breeding ranges are likely to shift northwards (section 4.2), which could mean increased inter-specific competition leading to declines. However, it is likely that these declines are not climate change caused as much as land-use change related.

Scrub species’ population trends exhibited a very weak negative association with the vulnerability index. This is not surprising since scrub species have a wide range of Vulnerability scores (see section 5.1). Some species’ predicted future vulnerability matches the current population trend for example: *Sylvia melanothorax* increased or was stable during the 1960-2000 period and is classified as least/moderately vulnerable to climate change, whilst *Locustella naevia* is currently declining and projected to be highly vulnerable to climate change. In contrast, *Sylvia undata* was strongly declining during the 1970-1990 period and yet is only classified as either moderately vulnerable or vulnerable to climate change. Here lack of data (unknown trend for the 1990-2000 period due to the unknown trend of the greater part of the population in Spain), as well as the scale of data used, are limiting my analysis. For example, this species is currently increasing in Britain where my models indicate increased climatic suitability in the future (see digital appendix).

Upland species exhibited a strong negative association between population trend and future climate change vulnerability. Climate change has been shown to cause species’ distributions to move to higher elevations (Wilson *et al.*, 2005). *Oenanthe xanthoprymna* for example is currently declining and is projected to be highly vulnerable to climate change. *Oenanthe oenanthe* is currently decreasing and projected to be moderately vulnerable, whereas

Monticola solitarus is currently stable and projected to be least vulnerable to climate change. Shoo *et al.* (2005b) found that species' populations that occupied territories at mid elevation were more likely to decline than those species' populations at higher altitudes. This is an interesting observation that indicates potentially complex processes operating that analyses such as undertaken in this Chapter cannot capture, thereby showing its limited application.

Stronger associations were found between the 1990-2000 population trend and future climate change impacts than the 1970-1990 period. The results in the previous section indicated a stronger relationship between population change and climate during the 1970-1990 period than for the 1990-2000 period. However, climate changed rapidly during the latter part of the 20th century (Dore, 2005; Hulme *et al.*, 2002), which may not have shown in the smoothed climate trends calculated for the 1990-2000 period (Gregory *et al*., 2009). Populations, however, may have started to respond to these changes. Juillard *et al.* (2004) examined the relationship between bird productivity during a particularly warm spring (as an indicator of future conditions) and population trends. They found a positive relationship between productivity during that year and population trends, concluding that long-term population dynamics was therefore related to global warming. Their conclusion is far too simple and does not necessarily follow on from their results. Nevertheless, their study suggests that the occurrence of climatic extremes, which are projected to increase in the future, may be more relevant to population changes than mean changes in climate.

5.3.5 Conclusion

Despite a few climate-vulnerability associations, the results are not conclusive in demonstrating a general effect of climate on species' population trends. The results are based on projected future changes in species' distribution. This may be misleading since changes in species' range size or location will also be determined by species' ability to disperse, whether the changes occur at the core of species' range or at its edge (Jarema *et al.*, 2009), and whether other factors interact or override projected climatic changes (such as habitat degradation or enhancement).

Fluctuations in population size may not be independent of long-term trends or even short-term trends. Indeed, a declining population may continue to decline, even if conditions improve, due to the effects from what is known as the 'extinction vortex' (Gilpin and Soulé, 1986; Fagan and Holmes, 2006). Fagan and Holmes (2006) analysed ten wild vertebrate populations' descent into extinction, to test theoretical predictions about the process of extinction. They found that

populations followed a logarithmic relationship between population size and time-to-extinction, and that the bird populations in the study followed this theory more closely than the other vertebrates in the study.

The results from these two sections show that a general climatic change effect on migratory bird populations is not observed. There was high over-dispersion in the ordinal regression models indicating that the models were missing important explanatory factors. The analyses indicate, however, that there is a large variation between species and that climate may be a factor in the population trends of some species. However, more detailed analyses would need to be undertaken to find the main drivers of population change. These results demonstrate that generalised statements may not always be applicable when dealing with complex processes such as population fluctuations.

6. Synthesis & Discussion

Macroecological theory as well as empirical evidence from a plethora of studies suggests that ultimately, at broad scales, species' distributions are determined by climate. At finer scales and within climatic constraints, species' distributions are constrained by abiotic and biotic factors. There is much debate amongst ecologists about the exact scale at which different factors become important. It has been argued that at coarse resolutions and over large scales, biotic factors as well as some abiotic factors become less important than climatic controls (Chapter 2). This has led to the widespread use of climate envelope models, niche models or species distribution models (SDM). These techniques for studying species' distributions have become more prevalent in recent years, in part because of the ease of such studies, and also because they are one of the most useful ways to predict the impact of climate change on species' distributions.

Climate change is now a mainstream concern as evidence grows of its occurring and of its noticeable effect on many aspects of species' ecology. Birds are one of the most studied taxa and a wealth of evidence shows that climate change is impacting on their phenology, ecology, distribution, and numbers (Chapter 2).

Migration is a common strategy for many bird populations (Berthold, 2001; Newton, 2008). Although, migration enables species to make use of the seasonal nature of certain parts of the globe, it is energy demanding and perilous. Migratory species may be more at risk from climate change than their resident counterparts, a concern heightened with the widespread decline of many long-distance migrants (Sanderson *et al.*, 2006); in particular because migrants rely on bioclimatically different areas, which may not change in the same way in response to climate change.

Many studies have examined the effect of current climate change on the timing of migration and breeding in birds, reporting earlier arrival on the breeding grounds and earlier egg laying in many short/medium-distance migrants, as well as some (but not all) long-distance migrants (Crick *et al.*, 1997; Gordo *et al.*, 2005). Similarly, many studies have forecast potential consequences of climate change on species' breeding ranges, including birds (Erasmus *et al.*, 2002; Huntley *et al.* 2006, 2007). However, as yet, no-one has examined the potential impact of climate change on the distribution of migratory birds in both their breeding and non-breeding ranges. Most modelling studies relating migratory bird species' distributions to climate have concentrated on the breeding ranges, with little research undertaken on wintering ranges (but see Martinez-Meyer *et al.*, 2004). However, weather

conditions, i.e. the fluctuations in climate, on the wintering grounds are crucial in determining population fluctuations and trends of several trans-Saharan migrant birds (Baillie & Peach, 1992; Gordo *et al.*, 2005; Jones *et al.*, 1996; Saino *et al.*, 2004a, 2004b). Changes in the extent and, particularly, the location of the wintering range could have marked effects on the future viability of populations of migratory species. For example, species believed to have relatively stable breeding ranges might decline as a result of large changes in the extent of the wintering range. In addition, a progressive shift apart of the breeding and wintering ranges might entail increased migratory distances and altered migration routes.

This thesis aimed to examine the potential impacts of climate change on the distribution and migration of Afro-Palaearctic migrant birds. This study was not exhaustive in the species used, concentrating on those migrants that have a large part of their breeding range in the Western Palaearctic and winter within the Western Palaearctic and in Africa. Moreover, only species' breeding and non-breeding distributions were examined, with no attempt to quantify changes along the migratory route or to their phenology. Finally, only broad scale changes in terms of magnitude and direction of shift in the face of climate changed were examined. The results are therefore coarse in nature as were the data used. This work entailed three main aims:

1) Model the present distribution of Afro-Palaearctic birds on their breeding and non-breeding grounds.
2) Project the distributions into future climate change scenarios and examine the potential impacts of climate change.
3) Assess the vulnerability of migrant birds to climatic change.

The first part of this Chapter recapitulates the findings of the thesis by answering and discussing the questions attached to these aims (section 2.2). The second part sets the results in the wider context, by discussing the likelihood of changes in an evolutionary context, and discusses the uncertainties and limitations of the study. Finally, future challenges are outlined.

6.1 Synthesis

6.1.1 Species distribution models: breeding and non-breeding ranges of Afro-Palaearctic migratory birds

Model selection

The development of species distribution models (SDM) is, to some extent, driven by the kinds of data available and the purpose of the models. Their performance will, in part, be the result of the accuracy and precision of the data used, the ability of the technique to describe the species-environment relationship, and the validity of the captured relationship (Guisan and Thuiller, 2005). Performance of a model is, in itself, an uncertainty because the definition of what constitutes a well performing model is subjective and depends on the ultimate purpose of the model. Moreover, because models are simplistic approximations of a "reality" (once again this depends on many things including the conceptions of the modeller), they are a balancing act between generality and accuracy (Heikkinen *et al.*, 2006).

All the questions researched in the first part of the thesis stem from one broad question: *Which model?* This question can be further broken down into: which variables describe the species-environment relationship best; and how are these variables related to species' distributions? This second question directly refers to the technique used to model species' distributions. There have been many studies comparing different modelling techniques (e.g. Elith *et al.*, 2006) but no clear cut answer has emerged, leaving model testing an important part of the creation of SDM (Austin, 2007). Few studies have examined the importance of variable choice in SDM building though there have been some exceptions (e.g. Heikkinen *et al.*, 2006). Choice of predictor variable has many implications, including the conceptual validity of the model and its applicability over space and time (Araújo and Guisan, 2006).

These questions have to be tested and answered within the framework of the purpose of the model. Indeed, the validity of a model will differ if its purpose is merely to describe the species-environment relationship or if it is to be used in a predictive capacity (Araújo and Guisan, 2006). The aim of this thesis was to predict the potential effects of climatic change on migratory birds. Therefore, the models need to perform well in their predictive ability. The difficulty in measuring predictive ability (see Chapter 2 & 3), however, means that proxy qualities need to be used. Robustness (stability of a model) and generalisability, which entails making sure the models do not over-fit, are consequently important.

In section 3.1, the question of *how model section affects robustness and predictive ability* was investigated. Answering this question is a multi-step process. First, the choice of variables will be important because it determines the conceptual validity of a model. Second, performance of the models needs to be compared. This in itself is difficult, because there are many ways to select (and evaluate) a model.

The first step in this process was to determine a set of candidate predictor variables and then models, which should be ecologically meaningful in determining species' distributions and relevant to the purpose and scale of the model. Huntley *et al.* (2004) demonstrated that a small set of bioclimatic variables could produce an adequate depiction of the species-environment relationship at coarse resolutions. This choice of predictor variables in SDM has also been successfully used in other studies (e.g. Bakkenes *et al.*, 2002; Thuiller *et al.*, 2005a). The results from section 3.1, including the excellent fits of the models and the analysis from the simple models, corroborate the use of these bioclimatic variables and demonstrate the conceptual validity of this approach. However, my results showed that choice of predictor variables is species dependent, with the inclusion of seasonal variables important for migratory birds. Moreover, different explanatory variables are needed for the breeding or non-breeding grounds. Many studies incorporating vast numbers of species have used the same set of predictor variables for each species. I believe this is too simplistic and can introduce error and uncertainty into the predictions.

The results of the analyses undertaken in section 3.1 indicate that choice of model seriously affects robustness and generalisability. Choice of model is usually done via a model selection technique (see section 3.1.1). Analyses undertaken using a variety of commonly used techniques in model selection, more specifically AIC, AUC, data partitioning and independent data, revealed that these methods differed in their model selection. Furthermore, certain methods did not necessarily choose the most robust model in terms of precision and accuracy (Walther and Moore, 2005). The approach which selected the most robust models was cross-validation (partitioning the data several times to find the most precise and accurate model), a result also found by Maggini *et al.* (2006). These models were shown to reduce uncertainty when extrapolating. Indeed, comparisons of the future projections built on part of the data to those built on the entire data set, showed that robust models were more precise and accurate (Fig. 3.2 & 3.3). Moreover, these models were better in extrapolating onto independent data sets (Table 3.6).

One incidental finding from section 3.1, however, was that, in the ecological literature, there is a lack of studies investigating the relationship between model selection procedures and predictive ability. Furthermore, most studies using SDM do not concern themselves with

a proper evaluation of their models. Consequently, there is no set evaluation framework. In a recent paper, Elith and Graham (2009) voiced this concern and called for modellers to start asking more questions about their models and methods. Their concerns mainly involved the modelling techniques used. However, I think their concerns apply more widely to the entire framework of species' distribution modelling.

The choice of modelling technique for SDM is still difficult because there is a vast choice of methods available and the choice of method(s) should take into account the data available, the purpose of the model and ecological theory, so that the shape of the modelled response is rational (Austin, 2007). With these caveats in mind, methods were sought that not only fulfilled these criteria but also had a large evidence base surrounding their use, to enable acknowledgement of their limitations, thereby minimising uncertainty.

Regression-based techniques that can model complex responses have been shown to be among the best for predicting species' distributions (Elith *et al.*, 2006; Heikkinen, *et al.*, 2006), as niche theory and empirical evidence show that unimodal response curves are prevalent (Austin, 2007). Generalised Additive Models (GAM) and Climate Response Surfaces (CRS) are two such techniques. In the ecological literature, however, GAM have a larger evidence base than CRS and have been shown to perform well under a variety of circumstances and for a variety of purposes. Generalised Linear Models (GLM) are another regression based technique that has been shown in some studies to be more transferable (Radin *et al.*, 2006), despite it being more restrictive in its ability to model complex relationships.

In sections 3.2 and 4.1, I examined the performance of these different modelling techniques and looked for differences in simulation and projections. Testing the performance of each method was secondary, as all these techniques have been shown to perform well. My main questions were *how the methods differed;* and *whether different modelling methods produce different future projections?* These questions are necessary to quantify the uncertainty in the modelling procedure and choose the method(s) that minimise that uncertainty.

Araújo *et al.* (2005b) and Pearson *et al.* (2006) also examined these questions. Both found prediction and performance differences between methods, though Pearson *et al.* (2006) found that these stemmed from the type of data input and the assumptions of each modelling technique. Therefore, I expected that there would be differences in performance and output and that the differences would be minimised between similar techniques.

In section 3.2, I explored differences in simulations in terms of their performance (fit, robustness and predictive ability) and in terms of their output (raw values, simulated

prevalence and spatial differences). The results showed that model performance and output differed among methods. Specifically, the results showed that CRS had better model fit (higher AUC values) than the other methods (Table 3.7). This is because CRS employs locally weighted regression, which makes it excellent for describing the data available. One concern with this is that it over-fits the data, making it less robust as well as less transferable. CRS produced robust models, though GAM was the more robust of the two methods (Fig. 3.8). The distinction between the two in this case was difficult as it involved a trade-off between precision and accuracy. GAM and CRS performed equally well in predicting to an independent data set (Fig. 3.9). CRS's curve-fitting did not seem to affect its robustness in extrapolation negatively, corroborating the study by Beering *et al.* (1995). GAM have been shown in numerous studies to perform well, not only in simulating current distributions (e.g. Araújo *et al.*, 2005a; Elith, *et al.*, 2006) but also in projecting onto new data (Hijmans and Graham, 2006). GLM, by contrast, consistently performed worse than the other two methods despite its demonstrated usefulness in some studies (Radin, *et al.*, 2006; Elith and Graham, 2009). The differences in performance are slightly misleading because different methods performed better for certain species. Although different predictor variables were used for different species, one over-arching technique was sought for all species. The reasons for choosing one technique for all species were 1) for simplicity, 2) to conform to other studies and 3) to keep the assumptions and uncertainties limited.

Comparisons of the outputs of each method have rarely been investigated in the literature but are nevertheless important in determining sources of error (Barry and Elith, 2006; Lobo *et al*., 2007) and in giving a better understanding of the models' workings (Elith and Graham, 2009). In terms of raw output, GAM and CRS were more similar than GLM. This was the case with current (section 3.2) and future simulations (section 4.1). Species' simulated prevalence was compared between each method and with observed data. GLM greatly over-predicted prevalence in most cases and CRS closely simulated observed prevalence (Fig. 3.6). The biome analysis undertaken in section 3.2, aimed to investigate how well each method characterised climatic niche and whether there were any systematic spatial differences between methods. There were systematic differences (Fig. 3.7). On the breeding grounds, all methods underestimated prevalence in temperate broadleaf and mixed forests, temperate coniferous forest, and Mediterranean forests and scrub, and overestimated prevalence in boreal forest/taiga. On the non-breeding grounds, all methods underestimated prevalence in Mediterranean forests and scrub and overestimated in tropical and sub-tropical dry broadleaf forests and boreal forest/taiga. Overall, GLM simulations of prevalence in different biomes was different to the observed data whilst GAM and CRS were generally

more in agreement with the observed data and with one another. The sum of these results broadly concur with the conclusion by Pearson *et al.* (2006) that differences stem from the assumptions of each modelling technique. These differences in characterisation of the species-environment relationship are also, in all likelihood, what generate the different future projections (section 4.1). The differences in future projections were analysed by comparing the different measures of change between future and present simulations commonly used in climate impact studies (e.g. changes in range extent and overlap between current and future simulated distributions) and by comparing the output of the future simulations. Statistically, the values of each measure of change obtained from each method were significantly different (section 4.1.3). However, the magnitude of change as well as the direction of change was generally the same between CRS and GAM, whilst GLM was sometimes different. When testing such a large number of models and species, it is possible to over interpret the statistical significance of results. It is, therefore, useful to examine statistical effect size (Field, 2005) but more valuable to compare actually differences in the models output. Comparison of the future simulated maps also indicated that GAM and CRS were more similar in their projections than GLM (Tables 4.1-4.8). These findings are not surprising and are consistent with other research (Thuiller, 2003; 2004; Araújo *et al.,* 2005b; Pearson *et al.,* 2006). Unfortunately, these differences contribute to the uncertainty in future projections and point to caution in interpreting the potential impacts of climate change as projected by such methods.

There are three ways of dealing with this variability and reduce the uncertainty in model specification. First, is to select the best model from the framework of models chosen (Thuiller, 2003; 2004). In this case, either GAM or CRS could be chosen. When presenting the species distribution models in section 3.3, I chose to present results from GAM but provide results from CRS and GLM in the digital appendix. Second, is to undertake model averaging. Model averaging involves "calculating a weighted average of parameter estimates" (Johnson and Omland, 2004; p.104) and is a common practice in ecology and evolution, though has yet to feature in the SDM field. Model averaging reduces model selection bias and reduces the burden of reporting of numerous results. Future SDM studies may wish to explore this option. The third approach, which I chose, when presenting the results for the potential effects of climatic change, is the consensus approach. Using a multi-model ensemble or a consensus approach (Araújo and New, 2006) is an effective way deal with uncertainty in extrapolation. This approach has been shown to be effective not only for SDM (Araújo *et al.,* 2005b) but also for global climate models (IPCC, 2007). Moreover, averaging model projections increase the accuracy of forecasts when better models rather than more models are used (Araújo *et al.,* 2005b).

Having decided upon a framework for modelling the breeding and non-breeding ranges of Afro-Palaearctic migrants, the question then is *can good SDM be constructed for the breeding and non-breeding ranges of Afro-Palaearctic migrant birds?* The answer to this question involves examination not only of measures of goodness-of-fit but also a spatial comparison between observed and simulated data. In terms of goodness-of-fit, breeding distribution models' AUC ranged from 0.798 to 1.00 and non-breeding distribution models' AUC ranged from 0.812 to 0.996, indicating that good models can be built (AUC values from 0.70-0.80 are fair, 0.80-0.90 are good whilst 0.90-1.00 are excellent (Swets, 1988)). AUC describes the discrimination ability of the models and is a threshold independent measure. However, to use the models' output effectively, a threshold needs to be placed on the raw probability values so that presence-absence maps can be generated. Imposing a threshold necessarily results in loss of information, and generates some classification errors which are measured by Cohen's Kappa (Cohen, 1960). The models' kappa values ranged from poor to excellent (see digital appendix).

In general, breeding range models were better than non-breeding range models. Overlapping breeding and non-breeding models resulted in accurately depicting areas where species were resident. I did not set out to model areas of residency but it is gratifying that these areas match up (see digital appendix). The better breeding models may be due to better quality data or a more constrained breeding climatic niche. Indeed, many researchers have found that more marginal climatic niches are better modelled (Brotons *et al.*, 2004; Segurado and Araújo, 2004). The quality of the non-breeding ground distribution maps varies, and in sub-Saharan Africa is coarse. The difficulty with the non-breeding distribution of migratory birds is that, although they may have a wide potential distribution, they may not occupy the entire suitable area; this is because, during the season, some species move around with favourable conditions or occupy specific areas at different times of the non-breeding season (Newton, 2008).

There are some systematic discrepancies between observed and simulated spatial distributions. These discrepancies arise from the fact that species' distributions are evidently not entirely constrained by climate. The models, therefore, often simulate species' distributions in areas from which, although climatically similar to areas where birds are present, the species is absent due either to historical factors, ecological and physical barriers or population size/dispersal issues (Newton, 2003). An example of this is that, for Mediterranean species, the models also simulate suitable areas in South Africa (Fig. 3.14).

The models also under-predict some species' distributions, most notably in the Nile region (Fig. 3.16). It is evident that habitat or meso/micro climatic variables, which have not been included in the models, are important. Although many authors have argued that climate is the overriding factor in determining species' distribution at large spatial scales (Huntley *et al.*, 2007; Luoto *et al.*, 2007; Thuiller *et al.*, 2004a), it is clear from these results that this conclusion may be too general.

Many authors have also questioned w*hat affects the performance of SDM?* I investigated this question in section 3.3.3. I looked at various aspects of species' ecology which might impact on how well they were modelled, including their prevalence across the range, the major biome in which they were found and preferred habitat type. I found that species with high prevalence were less well modelled, as were wetland and coastal species. Species residing in distinct climatic/vegetation areas (biomes) such as boreal forests were best modelled. These results corroborate findings in the literature (see section 3.3.3).

It has been argued that ecological/geographical attributes significantly affect model performance and therefore should be taken into account when making use of SDM. Although the concluding part of that view is correct, I believe the first part of the argument is false: it is not the ecological/geographical attributes that affect model performance but model specification which is at fault. Clearly, those models are lacking important factors explaining species' distributions or are built on the wrong variables all together. I acknowledge that for some species, models based purely on climate create a partially inaccurate simulation. However, the models are still good overall, and a perfect model is an oxymoron. Moreover, for the purpose of the model, which is to project future range change due to climatic change, as well as the scale, a bioclimatic model is necessary. Projections of future land-use/land cover change, once they become more widespread and realistic, will make welcome additions to species' distribution modelling.

6.1.2 Potential impacts of climate change on the distribution and migration of Afro-Palaearctic migrant birds

Variations in the output of species distribution models are due to the models and methods used to build SDM and the result of the models used for the creation of the environmental data (Peterson and Nakazawa, 2008); more specifically, due to the future climate models and scenarios (Beaumont *et al.*, 2008). Because we don't know what the future climate will be like, a range of potential future scenarios are generated which (hopefully) span the range of plausible future climates. This range of future climates is the product of different emission scenarios and different general circulation models (GCM) (Chapter 2). The combination of the different climate models quantifies the uncertainty in how climate works whilst the different emission scenarios accommodate the uncertainty surrounding future social, technological and political change.

I chose A1B and A2 emission scenarios, which are medium and extreme in the spectrum of emissions scenarios (Nakicenovic *et al.*, 2000). Aside from data availability issues, these scenarios were preferred because recent evidence is that greenhouse gas emissions are increasing at a faster rate than in previous decades which may mean that current estimates of future emissions have been underestimated (Canadell *et al.*, 2007; Raupach *et al.*, 2007).

To reduce the uncertainty surrounding the climatic element, the AR4 report uses different climate models as an ensemble; both to present the range of possibilities but also as a multi-model mean (IPCC, 2007). Ensemble forecasts quantify the uncertainty in forecasts by providing a range of values and reduce the uncertainty in model projections (when using consensus models and multi-model means) because the multi-model average reduces bias caused by individual models (Araújo and New, 2006; Beaumont *et al.*, 2008; Meehl *et al.*, 2007; Randall *et al.*, 2007). I have, therefore, presented results in Chapter 4 first as a multi-model mean (average of both SDM and three GCM), then as individual results to show the range of possible outcomes.

Given the variation in possible outcomes and the effort undertaken to minimise the uncertainty (use of consensus models and robust models and techniques), *how will the projected climate change affect migratory birds?* The individual species' results in the digital appendix show the huge variation amongst species in potential distributional changes due to climate change. Evidence from palaecological studies show that species have responded individualistically to past climatic change (Huntley, 1991; Stewart, 2008; Willis *et al.*, 2007) and are therefore likely to do so in the future. Despite these variations general trends can be

found and are reported in section 4.2. In section 4.3 the *differences between migratory groups* were investigated. Species were split into short-distance migrants (European or E migrants), long-distance trans-Saharan (T) migrants, and 'split-strategy' (S) migrants, those species with non-breeding ranges above and below the Sahara desert. This last classification is, of course, a simplification, since it takes into account partial migrants or species that have populations that migrate to different areas. If time and necessary data had been available, it may have been useful to undertake more detailed analyses for this group. However, as stated in the introduction to this Chapter, this is not an exhaustive work on migrant birds and climate change. In the following paragraphs, I summarise the results presented in Chapter 4.

Differences between future projections of climate change and trajectory of responses

There are consistent differences in future projections made using the different SDM, GCM and emission scenarios (e.g. Fig. 4.4 & A3). Generally, GAM and CRS project climate change effects in a similar direction of change but different magnitudes. Predictions of relative range extent assuming full dispersal (R) and overlap between future/present distribution (O; also seen as relative range extent assuming no dispersal), were more 'positive' for GAM than CRS, showing less reduction in O and a greater variation in R values with a higher mean value. Consequently, GAM project greater shifts in range as well as greater future 'migration distances'. Mean direction of range shift is in the same direction (North for the most part on the breeding and non-breeding grounds) but is of different magnitude (East-West tendencies) depending on the method and climate data used. GCM also contributes to these differences with GAM and CRS having more similarities using GFDL than with the Echam or HadGEM (Fig. 4.14-4.19). GFDL generally projects the most impact with greater migration distances, lower O and R values. HadGEM provides a middle of the road projection and Echam the most 'positive' projection. These differences are consistent with the observations from the AR4 report (Solomon *et al.*, 2007).

The results stemming from the different emission scenarios (A1B and A2) were very similar especially for the 2025 time-slice. In Beaumont *et al.'s* (2008) review of the use of future climate change scenarios in SDM, the authors report that during the early part of the 21st century, the projections from different emissions scenarios are similar. For the 2085 time-slice, A2 generally produces a 'worse' scenario in terms of overlap and shift in range.

The results also showed different trajectories of species' response to climate change through time. Changes in species' ranges were either linear (progressively worse; e.g. Fig. 4.4a) or non-linear (e.g. range reduction for 2025 and 2055 then increase in range in 2085; see

Fig 4.4b). Harrison *et al.* (2003) also report this finding. The Millennium Ecosystem Assessment (MA, 2005) reports on the common occurrence of non-linear changes in ecosystems and services. Non-linear effects can be generated by climate change if there are different land-atmosphere feedbacks (MA, 2005). Another explanation of non-linear trajectories is based on the movement of the suitable climatic window across space (see section 5.1.4). However, it is difficult to predict species' responses to such changes. Indeed species may respond to improving conditions after they have declined by either new range changes or population increases. Lister and Stuart (2008) report that, during the late Pleistocene, *Megaloceros giganteus* did not succeed in recovering all its former range during improving climatic conditions.

Projected distribution change

Breeding distribution

For the majority of species, range extent (R) is projected to decrease (Fig. 4.4b), by between 2-5% on average with maximum range reductions of 50% (Table 4.10). Individual model predictions forecast potentially greater range reductions than the average (Table 4.12, 4.14 and 4.16). For about 27% of species, however, climatic suitability on the breeding grounds increases, resulting in projected increased range extent. There were differences between migratory groups with S migrants having great reductions in R, while S and E migrants either had no change or increasing range extents (Fig. 4.11).

Evidence of range contractions due to current climatic change is scarce but has been documented for some butterfly species (Franco *et al.*, 2006; Thomas *et al.*, 2006). Southern range boundaries of some birds are limited by temperature and water availability. Böhning-Gaese and Lemoine (2004) suggest that anthropogenic activities such as irrigation and man-made water bodies effectively alter this limitation on birds' southern range margins.

Although some studies have documented range expansion of birds' breeding ranges (reviews: Newton, 2008; Parmesan and Yohe, 2003), there are a number of reasons why species may not expand their ranges, even if climatic conditions are favourable. The reasons include demographic factors, genetic factors, ecological factors, such as habitat availability or species interactions, and physical barriers. Another important point is that range expansion usually requires contiguous suitable range. The European landscape is highly fragmented and may curtail any potential range expansion. Travis (2003) used a simulation to show that fragmentation will exacerbate climate change. Furthermore, some of my models simulate

newly suitable ranges far from current distribution. This is mainly the case for species with small ranges. For these species, values of R may therefore exaggerate range change. This is one of the reasons why it is useful to look at the overlap areas between current and future suitable range. Overlap values show that, on average, about 50% (with a range of 10-90%) of species' current range remains suitable in the future (Table 4.10).

Species' breeding range, regardless of species' migratory behaviour, is projected to shift northwards, except for species with a breeding range centroid lying between 1° and 10° latitude that are expected to shift south-east (Fig. 4.5). This finding is similar to all studies projecting future climate change scenarios. Although climate may indeed provide suitable conditions further north, photoperiod may limit the extent to which species will be able to make use of these areas (see Coppack & Pulido, 2004).

The distances between current and future centres of range are projected to be about 130-1200 km (Table 4.10) regardless of migratory group. Current evidence is that birds' distributions have moved northwards by 19 km in the UK in the period 1970-1990 (Thomas and Lennon, 1999), 18.8 km in Finland for the same period (Brommer, 2004) and by about 91 km in France between 1989-2006 (Devictor, 2008). Devictor *et al*. (2008) showed that this polewards shift was lagging behind climate change by about 183 km.

Non-breeding range

For the majority of species, R is projected to increase in future time period (Fig. 4.4d), with non-breeding ranges for some species expected to double. However, some species are projected to have non-breeding range extents half the size of their current extent. Most notably, many areas in East and South Africa are projected to become unsuitable for many species (digital appendix). East Africa is currently a 'hotspot' for Afro-Palaearctic migrants (Fig. 4.7) so range contractions in that area may have dire consequences. For many species (though not all) the Sahel region is projected to remain favourable. There were differences between migratory groups in the magnitude of this projected range change with different trajectories for each group through time (Fig 4.11b).

There are a number of valid reasons why I think the projected future range expansion (greater climatic suitability to be more accurate) may be overestimated. The first reason is data driven. The distributions of non-breeding areas were coarse and covered large areas, potentially due to the uncertainty in where these species actually spend the non-breeding season. The SDM may not, therefore, capture species-environmental limits, leading to overestimation of range. Second is the issue of itinerancy of many species within Africa.

Certain species spend predetermined amounts of time in different parts of Africa whilst others follow favourable conditions (following rainfall for example). Therefore the use of annual and even seasonal climatic factors may not describe species' distributional limits. Finally, many species show non-breeding site fidelity, which may preclude these species from altering their non-breeding ranges. Indeed, the literature documents examples of species that, having expanded their breeding ranges, have conserved their non-breeding ranges, despite increases in migration distance (Sutherland, 1998; Newton, 2008).

Overlap values for the non-breeding areas are similar to those of the breeding areas (Table 4.11). However, there are differences between migratory groups. T migrants have less overlapping range than other species for the 2025 and 2055 time-slice projections (Fig. 4.12b). Unfavourable climatic conditions on the non-breeding grounds have been blamed for the decline of trans-Saharan migrants. My results provide further evidence that climate change may be in part responsible for these species' declines.

Range shifts are also projected to be greater for T migrants than for other species, ranging from 700 km to 1800 km (Fig. 4.13b). Direction of shift on the non breeding grounds depends on species' latitudinal distribution and therefore varies greatly among species. However, many species are projected to move in a northerly direction. Recently, the National Audubon Society has published a report detailing the changes in non-breeding distribution of American birds (National Audubon Society, 2009). They found a northwards shift of, on average, 56 km between 1966 and 2006 (National Audubon Society, 2009). However, they report greater range shift for some species; for example, *Megrus serrator* shifted 510 km and *Carpodacus purpureus* 504 km. It is possible, therefore, that species may extend their non-breeding ranges due to climatic change. However, many species' ability to winter further north is also due to human intervention, such as provision of food in gardens (Newton, 1998). In the Palaearctic- African migratory system, a further limit to northwards range expansion of the non-breeding range are the Sahara Desert and Mediterranean Sea, which pose formidable barriers to northwards range expansion, which do not exist in other migratory systems. However, in other systems, other barriers to dispersal may exist, such as mountain ranges.

Species richness and community turnover

The centre of species richness on the breeding range, under the full dispersal scenario, was projected to shift northwards in the future. For the intermediate periods of the current century (2025 and 2055) S migrants are projected to increase in number per grid cell compared with the present, whilst E and T migrants decline (Fig. 4.20).

On the non-breeding grounds, the results showed a general increase in species' numbers throughout the African non-breeding areas due to the projected increased climatic suitability. Centres of current winter avian species richness in Europe are to become more fragmented with more homogenisation in the rest of Europe (Fig. 4.7), with S migrants increasing more than other groups. This indicates that partial migrants may be clear 'winners' from projected climatic change.

I also examined migrant species' community turnover, by examining the different proportion of migratory categories per grid cell (Fig. 4.21-4.24). The results indicate changes in the composition of migratory avifauna in Europe and Africa. Increases are projected in northern Europe for E migrants for both breeding and non-breeding periods and increases in southern Europe and Africa for S migrants.

These results are coarse and are potentially only interesting as stepping stones for the formulation of hypotheses of change in species richness and community. Indeed, although species are likely to move individualistically, changes in community composition will depend on factors not taken into account in the analyses. First, it would make sense to include the entire avifauna in such an analysis, because resident species are likely to be important. Lemoine *et al.* (2007) examined changes in bird species richness at various sites within Europe for the period covering 1962-1992. They found an increase in proportion of long-distance migrants, a decrease in short-distance migrants and no change for resident species. Second, there are other controls to the formation of species' communities, such as species' niches, which are ignored in such an analysis. Finally, the results do not take into account the potential change in species' migratory behaviour (many species have become more resident over recent decades - see discussion below). Generally, most northerly breeding species are migratory, and the current and projected results are consistent with this. However, this is an area which warrants more research.

Migration distance

Average migration distances are projected to increase in the future compared with the present (Table 4.19). However, 2085 distances are projected to be smaller that those of 2055, which is due to an amelioration in climate suitability for many species in 2085. Distances vary among species but do not differ in terms of proportional change between migratory groups (Table 4.20-22). There were differences in minimum and maximum migration distances for trans-Saharan (T) migrants compared with the other groups. Indeed change in maximum migratory

distance was greater for T migrants in 2085 than other groups. In general most species' maximum distance increased.

Increases in migratory distance have been documented for some species (see Newton, 2008). However, migration distance is limited by 1) the amount of fuel a bird can carry, 2) suitable stopover sites, 3) genetic controls and 4) time. Therefore, increasing migratory distances from a progressive shift apart of the breeding and wintering ranges might have serious implications for migratory birds.

Minimum migration distances varied widely among species but, in general, distances decreased through either gaining "resident" cells or new non-breeding areas closer to their breeding grounds. There have been many reports of species wintering closer to their breeding grounds thereby reducing their migration distance (e.g. Valiela and Bowen, 2003; Austin and Rehfisch, 2005). Newton (2008) provides additional examples, as well as listing seven species (*Ardeola ralloides, Ciconia ciconia, Delichon ubrica, Falco naumanni, Motacilla flava, Nycticorax nycticorax* and *Pandion halietus*) that formally wintered in sub-Saharan Africa that now also winter in the Mediterranean region. The future models of non-breeding distributions for these species project newly suitable climate space in the Mediterranean region for all these species (digital appendix), giving credence to the models.

Projected changes in migratory distance, with the potential of new areas closer to the breeding grounds led me to the next question: *Will climate change impact on species' migratory behaviour?* Although potential changes to migratory behaviour are likely to depend on factors such as species' history and genetics, the analysis undertaken provides a start point for future investigation.

Changes in migration strategy

Change in migratory strategy was defined by gains or losses of non-breeding areas above and below the Sahara desert. Furthermore change in the proportion of 'resident' cells was also quantified and interpreted as changes in sedentary behaviour.

Depending on which SDM/GCM combination was used (Tables 4.25-27), one to four split-strategy migrants were predicted to lose their non-breeding areas in the Western Palaearctic, providing a possible selection pressure for these species to become solely trans-Saharan migrants. Another one to nine S migrants are projected to lose their African non-breeding quarters; this renders these species to be classified as solely short-distance migrants in the future.

About half of current obligate trans-Saharan migrants are simulated to gain non-breeding areas around the Mediterranean region. Species may establish new non-breeding areas and cut their migration distances and there is evidence of this occurring (see above). Changes in non-breeding location, however, may be in part determined by species' genotype. Indeed evidence from bird breeding range expansion shows that genetic change parallels successful range expansion (Berthold, 2001). Furthermore, species establishing new non-breeding areas also seem to have different genotypes (Bearhop *et al.*, 2005).

There is a lot of uncertainty surrounding these results on changes in migratory strategy, since different models simulated different changes on different species. I therefore, sought to see whether there were any consistent simulations. Table 4.28 lists species for which the models predict consistent non-breeding changes. Fourteen to seventeen species (depending on time-slice and emissions scenario) were consistently projected to change their 'migratory behaviour' from either trans-Saharan migrants to split-strategy migrants or split-strategy migrants to solely short-distance E migrants. However, these results only suggest that new climatically suitable areas will become available or that current areas are likely to become unsuitable. What the species do in response to these projections will depend on so many factors that it is difficult to provide even an informed guess.

Analyses of the changes in proportion of "resident cells" suggest that 55-61% of short-distance migrants may become more sedentary (Table 4.30). About half the split strategy migrants are projected to increase their proportion of resident cells. There is evidence of a trend towards reduced migratoriness in many bird species (Pulido and Berthold, 2004). My results also indicate that differences between species depend on where they reside. Species living in dry environments are projected to gain resident cells, as are those residing in temperate broad leaf and mixed forest; however, variation is considerable.

6.1.3 Species' vulnerability to climate change

Vulnerability

The ultimate questions for ecologists examining the potential effects of climate change on species are *which species are vulnerable, how are they vulnerable, why are they vulnerable, where are they vulnerable,* and *what can be done to reduce the vulnerability*? Before attempting to answer these questions, defining vulnerability is necessary. Turner *et al.* (2003) define vulnerability as "the degree to which a system, subsystem, or system component is likely to experience harm due to exposure to a hazard, either a perturbation or stress/stressors" (p. 8074). The vulnerability index created in the first part of Chapter 5 fulfils this definition by scaling species' vulnerability to climate change.

There are many ways that one could assess species' vulnerability to climatic change. Section 5.1.1 details examples of how this has been achieved in various studies. The prevailing finding was that there was no agreed framework to assess species' vulnerability to climate change. However, most studies utilise projected changes in distribution. Migratory species provide an extra complication because they utilise different areas during their life cycle and are prone to experience the effects of climate change on their breeding range, non-breeding range and during migration. Moreover, the effects of climate change on the breeding and non-breeding areas, such as loss of suitable areas, in either area are unlikely to be independent of each other. Indeed, in terms of population fluctuations, events in one area can result in changes in population size depending on what occurs in the other area (Sutherland, 1996). Furthermore, migration itself can result in population declines (Newton, 2006). The Vulnerability index was therefore created using changes in range extent and overlap of the area most affected by climate change, as well as the proportional change in migration distance. Before detailing which species are most vulnerable, it is of interest to ask what makes species vulnerable or *what factors impact on species vulnerability*? This question enables an examination of how the index quantifies vulnerability and also outlines, in general terms, what part of a species' ecology creates increased sensitivity to climate change.

For many species, increases in migratory distance contributed strongly to their vulnerability score (Table 5.2). Although there are examples of species lengthening their migratory route (see Newton, 2008), there is little evidence of the consequences thereof. Moreover, for the majority of Afro-Palaearctic migrants, their migration (route, stopovers, time, etc) is unknown. Much more is known of their spring phenology and the consequences of changes or non changes in arrival dates. However, if species do expand their breeding

ranges northwards, there is a very good chance of species facing greater migration distances which have the potential at least to impact negatively on species.

Reduction in range extent due to projected climate change contributed most to the vulnerability of forest dwelling species as well as those species breeding at high latitudes (boreal forest/taiga). This is worrying since forested areas already suffer pressure from habitat destruction. Furthermore, many forest birds are already declining (Gregory, *et al.*, 2007).

Low overlap between current and future climatic suitability, is projected to affect wetland, coastal and Mediterranean species more than other species. Schröter *et al.* (2005) also found that Mediterranean species were more sensitive to climate change than other species due to low overlap between current and future range. Their models, indicated similarly to mine, that although Mediterranean species were projected to show high range expansion, expansion was unlikely to be unimpeded. Furthermore, they report that these results were consistent with recent observations.

My results therefore go some way to address the why, where and how species could be classed as vulnerable to climate change. The next question is w*hich species are most vulnerable?* The results indicate that those species most at risk (i.e. those with the highest vulnerability scores) are upland or coastal species; trans-Saharan migrants; non-passerines; and species residing in tropical grassland, savannah/scrub or desert species (section 5.1.3).

In a recent study of the extinction risk of tropical rainforest vertebrates in Australia, Isaac *et al.* (2009) found that birds scored high on their vulnerability index which was based on range size, local abundance and habitat specificity. However, they also created a resilience index, based on reproductive output, climatic niche marginality and potential for long distance dispersal, and birds were one of the taxa most resilient to environmental change. Resilience is an important aspect of vulnerability analysis but is often overlooked in studies examining the potential extinction risk to climatic change.

Climate, population trends and resilience

Turner *et al.* (2003) suggest that there are three important concepts in vulnerability analysis: "entitlement" which can be interpreted as species' sensitivity, "coping through diversity" which entails species' responses and "resilience", a well known concept in ecology which takes into account the amount of perturbation a system can handle and its adaptive capacity.

Assessing species' vulnerability to climate change, therefore, needs to go beyond mere listing or projecting species' sensitivity to climatic change. We need to start achieving an understanding of how species respond, by examining 1) their response to climatic change, 2)

how important the stressor is to species (i.e. are other factors more important?), 3) the threshold at which the stressor becomes important, and 4) species' ability to adapt. Examining these aspects will enable a better understanding of species' responses and resilience to the projected stressor. The final two sections of Chapter 5 start to address these questions and give a better understanding of what climate impact studies using SDM can and cannot do. Indeed, many authors have used SDM to project species' vulnerability to climate change and infer their extinction risk (Bomhard *et al.*, 2005; Thomas *et al.*, 2004; Thuiller *et al.*, 2006).

Species' extinction risk will depend on population and metapopulation dynamics. It is pertinent, therefore, to ask *how much can be inferred from SDM in terms of population change?* Answering this question also enables the examination of 1) how species respond to climate, since bioclimatic SDM aim to measure species' climatic tolerance, and 2) how important climate is in shaping population trends. But not the above questions 3) and 4).

In section 5.2, recent population change was correlated with trends in climatic suitability as modelled by the SDM. Ecological correlates potentially impacting on population trends such as habitat or migratory category were also included in the analysis. Analyses were performed for all species and separately for passerines and non-passerines (as well as for a few individual species - Appendix IIId), linking breeding and/or non-breeding climatic suitability with and without time lags. The results (section 5.2.3) demonstrated that 1) climate suitability on breeding and non-breeding grounds was associated with population trends (improvement over null model), 2) time lags were evident, and 3) other factors were likely to be more important in some cases than climate (high over-dispersion in the models).

The overarching conclusion from this section is that bioclimatic models can be used in ways other than merely plotting species' simulated and potential distributions, though care needs to be taken not to over-interpret the results especially if testing multiple hypotheses. My results show that bioclimatic models cannot predict population change (see below), but can be used to explore the relationships between climate and population.

The results showed that breeding ground climate suitability was significantly positively correlated with non-passerine population trends (Fig. 5.14a). This was the expected relationship. Four to five years time lagged climatic suitability correlated with population trends (Table 5.14-15). Many authors have found evidence of lagged responses to climate change (see section 5.2). Analyses of passerine species, however, revealed a significant negative relationship between population trend and climatic suitability on the non-breeding grounds (Fig. 5.16b & 5.17b). Section 5.2.4 discussed the possible reasons this could occur.

Factors, such as change in habitat, will contribute to species' population trends; indeed, I found that habitat was an important factor in explaining population trend.

Furthermore populations are limited by a whole host of factors such as competition, disease, predators, as well as climate events (Newton, 1998). Although specific climate events such as a spell of unseasonal weather have resulted in changes in bird numbers (e.g. Baillie & Peach, 1992, Newton, 2007), multiple factors contribute to long-term population trends, making the contribution of climate change to change in population numbers difficult to discern.

Two related factors could explain the weak relationship between climate and population trends (apart from the explanation that climate may be important only for some species). First is the weakness of the climatic trends themselves and, second is the amount climate changed during the time period. Jiguet *et al.* (2007) tested whether species-specific variables, including climate envelope measures, and ecological and life history variables could predict recent bird population trends in France. They found that the climate envelope component important in population trend was the "thermal maximum" which captured 11.9% of the variance in the model. In section 5.2, average climatic suitability was used rather than any other measure. This may confound results since changes are unlikely to be even over a species' range.

Furthermore, climate has not changed that much between 1960 and 2000, but is projected to change much more according to the future climate change projections (IPCC, 2007). Following the results of Gregory *et al*. (2009), I investigated whether *there is any relation between past population change and projected future climatic change impacts*. It is possible that current species' population trends are tending in the direction of future climatic change. My results showed that, for some species, the 1990-2000 population trend was associated with future climate change vulnerability. Upland species and forest passerine species had significant negative associations with the vulnerability index (Table 5.25), indicating that declining species were also those more vulnerable to climate change and increasing/stable species were also those least vulnerable to climate change. This means that for those species, climate change may be having a noticeable effect on population numbers. It has been suggested that climatic change may be a driver of the decline of trans-Saharan migrants. The results do not reveal a significant association between the index and recent population trends of trans-Saharan migrants as a group (Table 5.22 & 5.24). However, the association was negative and, furthermore, the Vulnerability index rates trans-Saharan migrants as more vulnerable than other species (section 5.1.3). This indicates that climate is likely to be a factor contributing to population declines.

These results indicate that the picture is more complex than SDM use and analyses can portray. Species' population sizes are determined by a number of factors, climate being one of them. However, not all species are necessarily going to be affected by climate change. SDM

can portray species' potential sensitivity to climate change, and may be able to address species' response to climate change up to a certain point. However, used on their own they do not and can not address species' resilience or adaptive capacity to climatic change, nor can they answer the question *how likely the projected changes are*. Jiguet *et al.* (2006, 2007) attempted to find the threshold at which the stressor becomes important, and the ability of species to adapt. They used the heat wave in France during the summer of 2003 to examine birds' responses in terms of population change. They found that species' thermal range was a good predictor of population growth rates: species with broad thermal ranges had a greater resilience (of population growth) to high-temperature anomalies than species with narrow thermal ranges (Jiguet *et al.*, 2006). They also showed that climate envelopes could be used to deduce the important climate suitability component (thermal maximum) to population change (Jiguet *et al.*, 2007).

6.2 Discussion

The distributions of organisms on the globe are a result of ecology and history and consequently cannot be fully understood in isolation (Crisci and Katinas, 2009). Bioclimatic models describe but a component of species' distributions. They may not capture the true relationship between species and their environment because they lack some of the fundamental elements that shape distribution patterns and, also because the assumptions they are based upon are not always valid.

A fundamental tenet of niche modelling is that species are in equilibrium with their environment. Many bird species have expanded their ranges during the last few years (Newton, 2003). Therefore, some species may not yet be in equilibrium with their environment. Furthermore, species' niches are constrained by other factors than climate, such as species interactions or barriers, which, if these change, could also invalidate the estimated bioclimatic niche (Davis *et al.*, 1998). The consequence is that the entire species-environment relationship has not been captured. Species may therefore be able to reside in more areas than they currently do. The impact of this error is that the projections of future climatic change will be exaggerated for these species. The projections may also be spurious if, for instance, a species requires certain species (e.g. host plant) to survive. In these cases, these interactions need to be included in the analyses. However, Merrill *et al.* (2008) showed that, in butterfly species' distribution over an elevational gradient, lack of host plants at the high elevations constrained species' distributions, whereas climate at the lower range margin and not host plant availability constrained species' distributions. Factors affecting species' distributions are therefore more complex than niche modelling can capture. Habitat, or the presence (or absence) of other species, may, therefore, be important in shaping and determining species' ranges. Some studies clearly show that changes in species' distributions are related to change in land-use and land cover rather than climatic change (Kerbiriou *et al.*, 2009; Okes *et al.*, 2008). Bioclimatic models are based on the assumption that at coarse scales climate is the overriding factor and, hence, do not include habitat variables. Many studies have shown this to be the case (see Chapter 2). However, modelling at coarse scales also means that results are coarse in nature and, as such, have limited use.

SDM are useful in giving insight into how species may respond to climate change (Chapter 4) and allowing examination of the relationship between species and climate (Chapter 5). My results report different changes on the breeding and non-breeding grounds for migratory birds. It is difficult to project the actual responses of species to these changes because the impacts on the breeding and non-breeding grounds are not uncoupled.

Furthermore, changes along the migratory route will affect species. Although the findings reported in this thesis concentrate on, and are based on, potential changes of range size and range position, the responses of species to climatic change are likely to involve not only changes in distribution, but also changes in population size and genetics. The link between population and climate is not straightforward as my results clearly demonstrate and, as such, warrants more research.

Many pessimistic results are reported in the literature (Chapter 2) and in this thesis (Chapter 4), but some species will profit from climatic change. My results show that, for some species, range expansion and reduction of migratory distances may occur. Furthermore, theoretical models suggest that environmental fluctuations may enhance biodiversity through the creation of new ordered states (D'Odoric *et al.*, 2008). The difficulty is that the consequences of individualistic responses to change cannot be forecast, because SDM cannot capture inter-species relationships. The fossil record shows that species' distribution trajectories are asymmetric – they rise to a peak very rapidly then gradually diminish (Liow and Stenseth, 2007). The decline is caused by novel community-level interactions (Shuttle *et al.*, 2006). This pattern of change (range expansion followed by decline) has also been shown for genera of extant birds (Webb and Gaston, 2000). However, the lessons from the fossil record may not be valid for future time periods as novel climates which have no modern analogue are predicted to occur (Williams and Jackson, 2007).

The likelihood of niche shifts to climatic change is the biggest uncertainty in studies examining the potential impacts of climate change. The evidence from the past (Lister & Stuart) as well as from current studies (see Pearman *et al.*, 2007) is mixed: some species have shifted their ranges whereas, in others, niche conservatism has prevailed (Pearman *et al.*, 2007; Willis *et al.*, 2007). For those species that are likely to shift their range due to climatic change, evidence from empirical studies (Devictor *et al*., 2008; Menedez *et al.*, 2006) as well as from simulation studies (Mustin *et al.*, 2009) indicates that time lags will occur. If the modelled niche is correct and if the landscape is not fragmented, the likelihood of niche shifts in response to climatic change will depend on genetics, demography and dispersal.

The majority of SDM studies fail to incorporate realistic dispersal scenarios, including either an all or none scenario such as in this thesis. Scientists are starting to address this issue, which will be a continual challenge in the future. Recent studies have demonstrated that dispersal is complex, depending on dispersal ability along with, and also interacting with, demographic factors (Massot *et al.*, 2008) and/or inter-specific interactions (Brooker *et al.*, 2007).

Studies into the genetics of environmental change are in their infancy (Pulido and Berthold, 2004). In response to environmental change, surviving species will respond in a variety of ways. First, they may adapt through phenotypic adjustment. The ecological literature is full of examples of this occurring with changes in bird and migration phenology being the best researched taxa (Chapter 2). However, phenotypic plasticity may not always be sufficient and may be limited for long-distance migrants (Pulido and Berthold, 2004). Second, species may adapt through genetic selection. Empirical evidence indicates that some species may change under a strong selective pressure (Berthold *et al.*, 1992). Furthermore, Pulido and Berthold (2004) report that many authors have found extreme climatic events to be important as "selective agents" in bird populations. Given the current (albeit scant) evidence, they further suggest that birds have a high potential for adaptive evolutionary change (Pulido and Berthold, 2004). However, the potential of a species to evolve is dependent on a myriad of factors (De Mazancourt *et al.*, 2008; Hellman & Pineda-Krch, 2007) and is limited by the amount of genetic variability within a population (which may be small if populations are declining; Gilpin and Soulé, 1986), the potential for gene flow and time for mutations to arise. Finally, in the face of environmental change, species may move to areas where conditions are favourable; even in that case, microevolution may still be important (Berthold, 2001). The potential for adaptability (or not) will ultimately determine species' vulnerability and resilience to climate change. This fact contributes to uncertainty in the likelihood of future projections as determined by SDM.

There is still great uncertainty surrounding future projections of change. We do not know how the climate will change. This is the reason for so many climatic models and scenarios. Furthermore, all SDM and analyses of future change are based on changes in average climate. However, the frequency of extreme climatic events is also projected to increase in the future (Easterling *et al.*, 2000). It is frequently these extreme events that affect population size. The majority of climate assessments do not consider unlikely but high consequence events, such as the collapse of the "conveyor belt", the major ocean circulation systems (Schneider, 2003). These are events with low probability but are still worth quantifying since any risk assessment should include such events.

6.3 Conclusion and future challenges

This study provided the first broad analysis of the likely direction and magnitude of change of the distribution of migratory birds in response to climate change. It indicates different responses on the breeding and non-breeding grounds for many species. Further, it showed that for many migratory birds, a progressive shift apart of the breeding and wintering ranges is likely to increase migratory distances in future. Trans-Saharan migrants are projected to fare worse than other migratory groups from climate change. However, for many species newly suitable climatic areas may provide non-breeding areas closer to the breeding range, potentially allowing changes in migratory behaviour to evolve and enabling species to adapt to climatic change.

This study also shows the limits of climate impact studies using SDM. There is an urgent need to move away from coarse scale static modelling to new approaches including finer scale analysis, dynamic modelling and models incorporating population dynamics and changing land-use/land-cover (Anderson *et al.*, 2009; Mustin *et al.*, 2009; Willis *et al.*, 2009). Hierarchical modelling frameworks, using a set of models from coarse scale to fine scale, are also novel approaches which should be further extended as they allow more realistic projections of change including dispersal scenarios and even population change to be examined (del Barrio *et al.*, 2006; McRae *et al.*, 2008).

There is also a need to move to fine scale, species-specific analyses, incorporating life history elements, occupancy estimates, land cover and land-use change. We also need a better understanding of the physiological limits and adaptive capacity of species to climatic change. This understanding would enable analyses of species' vulnerability and resilience to climate change. Resilience of ecosystems is a well researched area in marine conservation (Gibbs, *et al.*, 2009; Hughes *et al.*, 2003) but is underrepresented for terrestrial ecosystems.

Finally, there is a need for climate change threats to be incorporated into IUCN Red List assessments. It is clear that many species are going to suffer from climatic change and including this threat in these assessments will allow for conservation action.

7. **References**

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